JAN 8 1942

Vol. 69 JANUARY, 1942 No. 1

Bulletin

of the

Torrey Botanical Club

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Published for the Club monthly except
July, August and September
by
THE SCIENCE PRESS PRINTING COMPANY
N. QUEEN ST. AND McGOVERN AVE.
LANCASTER, PENNSYLVANIA

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The Bulletin of the Torrey Botanical Club

Subscriptions, dues, and inquiries about back numbers should be sent to the office of publication, N. Queen St. and McGovern Ave., Lancaster, Pa., or to Dr. W. G. Whaley, Department of Botany, Barnard College, New York, N. Y. Correspondence about advertisements and circulation should be addressed to Dr. Michael Levine, Montefiore Hospital, New York, N. Y. Communications about exchanges should be sent to Dr. Harold C. Bold, Department of Botany, Barnard College, New York, N. Y. Manuscripts intended for the Bulletin should be sent to Dr. H. W. Rickett, The New York Botanical Garden, Bronx Park (Fordham Branch P. O.), New York, N. Y.

Claims for missing numbers must be made within 60 days from the date of issue.

The subscription price of the Bulletin of the Torrey Botanical Club is $6.00 a year except to active members of the Club. Of the annual membership dues, $3.00 covers a year's subscription to the Bulletin.

Torreya. Bimonthly; established 1901. Of the annual dues $0.50 is for a year's subscription to Torreya; price to non-members, $1.00. Manuscripts intended for publication in Torreya should be addressed to Dr. W. J. Bonisteel, Department of Biology, Fordham University, New York, N. Y.

Entered as second-class matter October 8, 1940 at the post office at Lancaster, Pa., under the Act of March 3, 1879. Accepted for mailing at the special rate of postage provided for in the Act of February 28, 1925, embodied in paragraph 4, section 538, P. L. & R.

BULLETIN OF THE TORREY BOTANICAL CLUB
69(1): 1–10 JANUARY, 1942

SECONDARY VASCULAR TISSUES OF THE OAKS INDIGENOUS TO THE UNITED STATES—II. TYPES OF TYLOSES AND THEIR DISTRIBUTION IN ERYTHROBALANUS AND LEUCOBALANUS

SIMON WILLIAMS[1]

The comparative abundance of tyloses in the earlywood pores in the heartwood of white oaks and their absence or sparsity in like structures in the heartwood of red oaks have long been utilized as aids in the separation of these two groups of woods.[2] *Leucobalanus*[3] species are said to possess extremely abundant tyloses, while in species belonging to *Erythrobalanus* they are considered to be sparse or wanting. The diagnostic significance of this discrepancy is admitted to be of limited application. Beyond question tyloses are the rule in most white oaks; their distribution in red oaks is so variable that their presence or absence, when considered alone, if of negligible value in diagnosis. However, in the course of a comparative study of the xylary structure of these two oak subgenera, several morphological types of tyloses were noted; if these are considered in conjunction with the abundance or scarcity of tyloses in oak, several apparently reliable indications of group relationships, in terms of species, are evident.

At the start it is admitted that the varying character of tyloses in *Quercus* and the distribution of the morphological types that can be recognized in the secondary xylem do not permit the segregation of species with the accuracy occasioned by the departures in the nature (shape and wall thickness) of the latewood pores. Nevertheless, this feature is of considerable value, serving as it does as a secondary character in the recognition of *Erythrobalanus* and *Leucobalanus* species and permitting meanwhile of further segregation of species in these two subgenera. It is the purpose of this investigation to illustrate and categorically group the various morphological types of tyloses encountered in a study of oak woods, to point out the structural departures which characterize each group, and to assay the diagnostic value of these tylosic types. Further, toward the end of the paper considerable space is allotted to a discussion of the chemical nature of the tylosic walls in *Quercus*.

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[1] The information incorporated in this paper has resulted from research by the author while a member of the Department of Wood Technology, New York State College of Forestry, Syracuse, N. Y. The author is now Research Technologist in the Bureau of Industrial Chemistry, University of Texas, Austin, Texas.

[2] Tyloses are uncommon in the latewood pores in *Quercus;* in this position they appear to be more frequent in *Erythrobalanus* than in *Leucobalanus.*

[3] The limits of *Erythrobalanus* and *Leucobalanus,* as understood in this discussion, were defined in the first paper of this series (2).

[THE BULLETIN for December (68: 609–694) was issued December 1, 1941]

TYPES OF TYLOSES IN THE XYLEM OF QUERCUS

Recognition of types of tyloses in *Quercus* is dependent in large measure on a variation in the number present in the cavities of the earlywood vessels and hence on the size of the tyloses, and on the thickness of the tylosic wall; stratification of the wall and pits, when present, serve as secondary characters. Three classes of tyloses may be recognized on the basis of the features enumerated above, as is indicated in table 1 and illustrated in figures 1 to 10, inclusive.

TABLE 1

Types of tyloses occurring in Quercus species

A—Tylosic walls extremely thin (under 2 microns)
1—Tyloses relatively sparse per vessel cavity (figs. 1 and 8).
2—Tyloses relatively abundant per vessel cavity (figs. 2 and 9).

B—Tylosic walls of "normal thickness" (3 to 5 microns); tyloses relatively sparse to moderately abundant per vessel cavity (figs. 3, 6, and 7).

C—Tylosic walls thick to extremely thick (5 to 50 microns), not infrequently stratified and pitted; tyloses sparse to abundant per vessel cavity (figs. 4, 5, and 10).

DISTRIBUTION OF TYLOSIC TYPES IN LEUCOBALANUS

Information on the types of tyloses and the abundance of tyloses in *Leucobalanus* are incorporated in table 2.

In *Leucobalanus*, the general statement can be made that tyloses are extremely abundant; they are usually present in all of the earlywood pores with the possible exception of a few of the last-formed pores, and are predominantly of Type B (see table 1). Exceptions occur to this rule, but they are few in number. *Q. bicolor* Willd., a chestnut oak, appears to possess tyloses of Type A, but Type B tyloses (of the kind which characterize *Q. alba* L.) may be present. Tyloses are sporadic in *Q. montana* Willd., some samples being almost devoid of these structures. *Q. sadleriana* R. Br. Campst., the only chestnut oak on the West Coast, had very few tyloses in the one sample studied. The remaining chestnut oaks, *Q. prinus* L. and *Q. muhlenbergii* Engel., possess abundant Type B tyloses, however, so it is difficult to generalize about the type common to this group. Nevertheless, there does seem to be a nebulous relationship in the nature of the tyloses in the chestnut oaks which further study might substantiate.

DISTRIBUTION OF TYLOSIC TYPES IN ERYTHROBALANUS

In table 3 are embodied data on the types of tyloses and the abundance of these structures in *Erythrobalanus*.

Explanation of figures 1–5

FIG. 1. *Q. bicolor* Willd. Illustrating Type A1, in cross section. FIG. 2. *Q. velutina* Lam. Illustrating Type A2, in cross section. FIG. 3. *Q. stellata* Wang. Illustrating Type B, in cross section. FIG. 4. *Q. arizonica* Sarg. Illustrating Type C, in cross section. FIG. 5. *Q. emoryi* Torr. Illustrating Type C, in cross section. Note pits in the tyloses walls. All × 225.

Figure 1

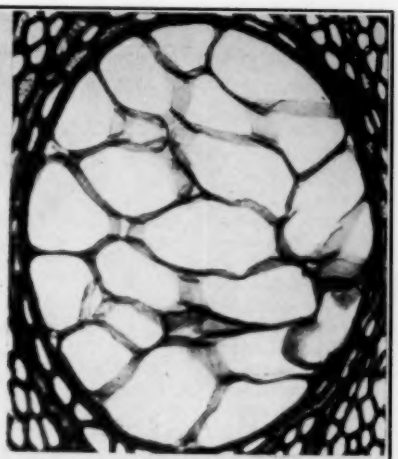

Figure 2

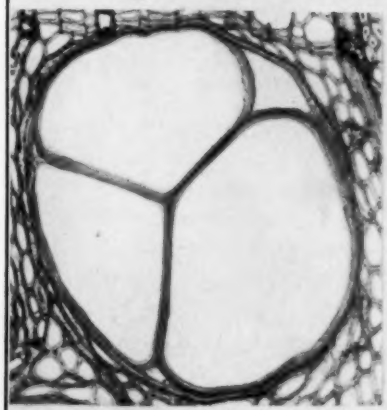

Figure 3

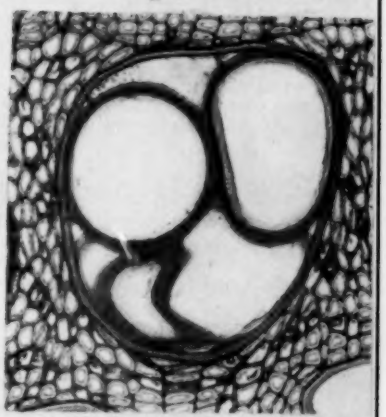

Figure 4

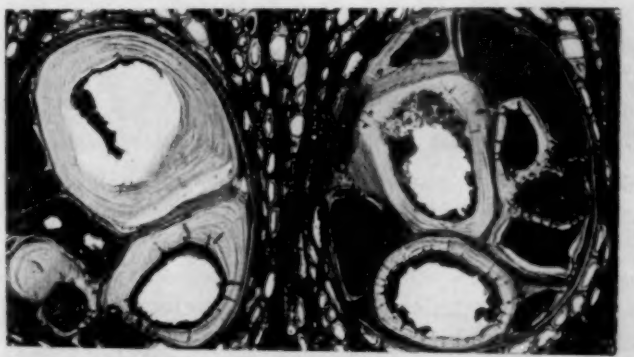

Figure 5

TABLE 2

Types and abundance of tyloses in Leucobalanus

Species	Type	Abundance
Q. alba	B	the rule
Q. bicolor	A1	the rule
Q. durandii	B	the rule
Q. garryana	B	the rule
Q. breweri	B	the rule
Q. lobata	B (A2)[a]	the rule (A2 very rare)
Q. lyrata	B	the rule
Q. macrocarpa	B	the rule
Q. montana	A1 and B	sporadic
Q. muhlenbergii	B	the rule
Q. prinus	B	the rule
Q. sadleriana	B	extremely sparse
Q. stellata	B	the rule
Q. utahensis (gambellii)[b]	B	the rule

[a] The type indicated in parentheses occurs only sporadically and never in any abundance.

[b] The nomenclature of this and closely related species is extremely confusing. Two of the samples were submitted as *Q. gambellii* Nutt. Two others were identified as *Q utahensis* Rydb. Investigation revealed that there is no certain way of distinguishing the various species and varieties, although *Q. gambellii* is generally regarded as the shrubby form. To simplify this taxonomic problem for use in this study, all samples submitted were considered under one heading.

Analysis of this information brings out the following facts:

1. Nine red oaks have tyloses throughout the heartwood at all times; the the following statements may be made for these *Quercus* species:
   (a) *Q. cinerea* Michx. and *Q. marilandica* Muench. have tyloses of Type B.
   (b) *Q. kelloggii* Newb. and *Q. ellipsoidalis* Hill are characterized by Type A tyloses, as a rule.
   (c) *Q. arizonica* Sarg., *Q. douglasii* Hook. et Arn., *Q. dumosa* Nutt., *Q. emoryi* Torr., and *Q. engelmannii* Greene possess Type B and Type C tyloses in admixture. Type C is dominant in these oaks with the exception of *Q. douglasii*. Note should be made at this time that these five oaks are xerophytic species occurring in southwestern United States or in California.
2. *Q. oblongifolia* Torr., *Q. hypoleuca* Engel., *Q. reticulata* H. B. K., also xerophytic species from the Southwest, possess Types B and C tyloses in abundance in the heartwood; there is every reason to believe that these Types would be found the rule in these three species were a sufficient number of samples available for examination. Together with the five species enumerated under 1 (c), they therefore may be considered as constituting a natural group of eight species in which tyloses are entirely comparable.
3. In *Q. agrifolia* Nee, *Q. chrysolepis* Liebm., *Q. wislizenii* A. DC., *Q. myrti-*

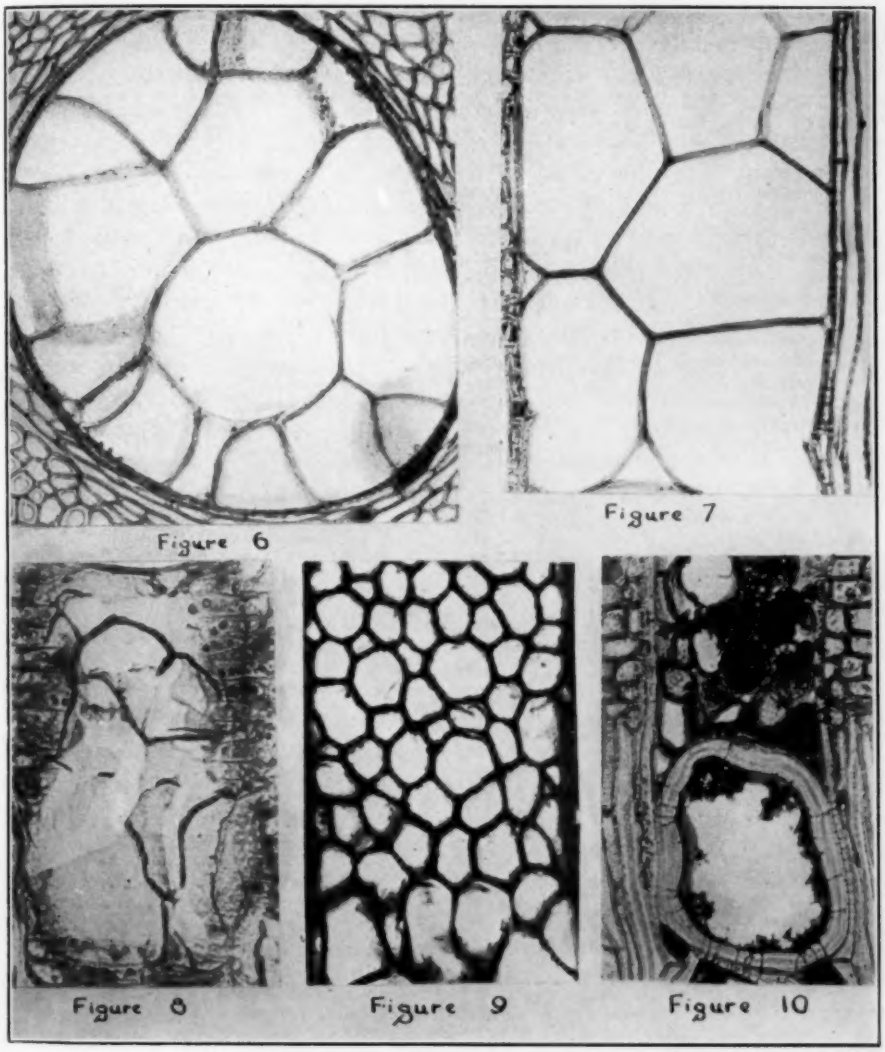

FIG. 6. *Q. prinus* L. Illustrating Type B, in cross section. Note that tyloses are more abundant than in figure 3. FIG. 7. *Q. stellata* Wang. Illustrating Type B, in longitudinal section. FIG. 8. *Q. bicolor* Willd. Illustrating Type A1, in longitudinal section. FIG. 9. *Q. velutina* Lam. Illustrating Type A2, in longitudinal section. FIG. 10. *Q. emoryi* Torr. Illustrating Type C, in longitudinal section. All $\times 225$.

TABLE 3

Types and abundance of tyloses in Erythrobalanus

Species	Type	Abundance
Live Oaks		
Q. agrifolia	A2	sparse
Q. arizonica	C (B)[a]	the rule
Q. chrysolepis	absent	----------
Q. douglasii	B and C	the rule
Q. dumosa	B and C	the rule
Q. durata	B and C	sparse
Q. emoryi	C (A and B)	the rule
Q. engelmannii	B and C	the rule
Q. hypoleuca	B and C	sparse
Q. myrtifolia	absent	----------
Q. oblongifolia	B and C	abundant
Q. reticulata	B (C)	sparse
Q. virginiana	A2	sparse
Q. virginiana geminata	absent	----------
Q. wislizenii	absent	----------
Deciduous Oaks		
Q. borealis maxima	A2 (B)	sparse
Q. catesbaei	A2 (B)	sparse to sporadically abundant
Q. cinerea	B (A2)	the rule
Q. coccinea	A2 (B)	sparse to sporadically abundant
Q. ellipsoidalis	A1	the rule
Q. ilicifolia	absent	----------
Q. imbricaria	A2 (A1, B)	sparse
Q. kelloggii	A1 (A2)	the rule
Q. laurifolia	A2	sparse
Q. marilandica	B	the rule
Q. morehus	absent	----------
Q. myrtifolia	absent	----------
Q. nigra	A2 (B)	sparse
Q. palustris	A2 (B)	sparse
Q. phellos	A2 (B)	sparse
Q. rubra	A2 (B)	sparse to sporadically abundant
Q. rubra leucophylla	A2 (B)	sparse to sporadically abundant
Q. rubra triloba	A2 (B)	sparse to sporadically abundant
Q. shumardii	A2 (B)	sparse to sporadically abundant
Q. velutina	A2 (B)	very sparse
Q. vaccinifolia	B	

[a] The type indicated in parentheses occurs only sporadically and never in any abundance.

folia Willd., and *Q. virginiana* Mill., although tyloses are present in the heartwood, they are extremely sparse and of Type A2.

4. In the eastern deciduous red oaks (*Q. marilandica*, *Q. cinerea*, and *Q. ellipsoidalis* excepted—see under 1 (a) and (b)—tyloses are very sporadic; they may be abundant in a given ring and sparse or lacking in the next, or absent altogether throughout the sample. When tyloses are present, Type A2 is always predominant in this group. Types B and C may occur but wherever these structures are found in a given ring, Type A2 is always more abundant, even though it is not present in all of the pores.

CHEMICAL COMPOSITION OF TYLOSES

The morphological variation and the fluctuation in the abundance of tyloses that permit of the recognition of tylosic types in American oaks has naturally led to the question as to whether or not these departures find expression in the chemical composition of the tylosic walls. Obviously, owing to the inconstancy of tylosic wall thickness from species to species, as discussed above, quantitative differences must occur. As this is clearly evidenced by microscopic examination, little would be added to the diagnostic significance of the tylosic groups listed in Table 1 by accumulating the exact quantitative data necessary to define these variations in tylosic wall thickness. Therefore, the chemical composition of tyloses as they occur in *Quercus,* discussed below, is based entirely upon qualitative analyses.

Isenberg (1), in a microchemical study of the tyloses occurring in hardwoods, concluded that three kinds appear to exist in terms of chemical composition, viz:

(1) Those with very thin walls composed chiefly of lignin to which are possibly added, on the inside, small irregular patches of cellulose. Example, *Fraxinus* spp.

(2) Those with a thin cellulosic layer within a layer of lignin. Example, *Catalpa speciosa* Ward.

(3) Those which possess a somewhat thicker layer of cellulose within the layer of lignin, with an inner layer of lignin (not visible in untreated sections) in turn deposited on the cellulose. Example, *Q. alba* L.

Isenberg designated this last condition as the oak type. Unfortunately, he examined the tyloses in but three species of oak (*Q. alba* L., *Q. dilata* Lind., and *Q. engelmannii* Greene[4]); because of the information already recorded in this paper relative to the varying nature and abundance of tyloses in domestic oaks, it may rightly be assumed that Isenberg's work was based on too few species of *Quercus* to give any true picture of the qualitative chemical nature of tyloses in this genus. It has therefore seemed advisable to repeat with certain minor changes the qualitative tests run by Isenberg on the species in question and to extend these to a sufficient number of additional species to represent all of the tylosic classes listed in table 1.

Materials and Techniques Employed in Determining the Chemical Composition of Tyloses in Quercus. Tyloses were examined in the following species:

(a) *Q. bicolor* Willd., *Q. montana* Willd., *Q. kelloggii* Newb., and *Q. ellipsoidalis* Hill, representing Type A1. *Q. coccinea* Muench. and *Q. velutina* Lam., representing Type A2.

(b) *Q. stellata* Wang., *Q. alba* L., *Q. cinerea* Michx., and *Q. marilandica* Muench., representing Type B.

[4] Isenberg makes no mention of the fact that *Q. engelmannii* has thick-walled tyloses in admixture with those of the type which feature *Q. alba.*

(c) *Q. emoryi* Torr., and *Q. arizonica* Sarg., representing Type C.

Blocks were cut from the dry heartwood and were extracted with hot water until no further evidence of tannin could be detected by treatment with an aqueous solution of ferric ammonium sulphate. They were then stored in 20 per cent ethyl alcohol until needed. Sections twenty microns thick were prepared from these blocks. These were then examined under polarized light before chemical treatment, and after chemical treatment (a) to remove hemicelluloses and (b) after (a) followed by treatments to remove cellulose or lignin. The examination prior to exposure to chemicals served to indicate the predominantly crystalline and non-crystalline portions of the tylosic wall; the solvent action of the chemicals employed was revealed by the subsequent examination of the material.

The chemical treatment of the sections, to remove hemicellulose, cellulose, and lignin, respectively, were as follows:

1. Removal of hemicellulose. The sections were alternately treated with 0.5 per cent NaOH for one hour and 3 per cent H_2SO_4 for three hours, over a water bath.

2. Removal of cellulose. (a) Treatment as in 1, followed by immersion in an excess of 72 per cent H_2SO_4 on a glass object slide, the reaction observed meanwhile under a microscope. (b) Treatment as in 1, followed by immersion in Schweizer's reagent,[5] the reaction observed meanwhile under a microscope.

3. Removal of lignin. Treatment as in 1, followed by a two minute chlorination (with saturated chlorine water) and then by a two minute immersion in a solution of monoethanolamine in 95 per cent ethyl alcohol (3). The first section examined received one complete treatment, the second two, using the chemicals in the order named, the third three, etc. After treatment the section was thoroughly washed in distilled water and was then examined with a microscope. Finally, it was exposed to 72 per cent H_2SO_4, to gauge the extent to which the lignin had been removed by the above-mentioned reagents. Complete solution of the section in concentrated sulphuric acid, a cellulose "solvent," indicated the fact that the lignin had very nearly been completely removed.

Discussion of the Results of Chemical Treatment of Tyloses in Oak Wood. The test for hemicellulosic material in tylosic walls was entirely negative. Some changes may have resulted but no visible evidence of reaction was discernible other than a slight swelling of the wall and a general increase in the plasticity of the sections. Nor did this treatment have any observable effect on the rate with which cellulose and lignin solvents reacted subsequently.

[5] It is recognized that cellulose may not be appreciably removed from lignified walls by this reagent.

Treatment with cellulose and lignin solvents yielded more conclusive evidence of the nature of the tylosic wall; this evidence may be summarized as follows:

1. The tyloses of Type A1 proved to be analogous to those of Isenberg's Class I. The bulk of the wall in this instance appeared to consist of lignin which was bounded exteriorly (toward the cavity) by an extremely thin layer of cellulose. Under the polarizing microscope, there was a slight indication that a third layer of lignin was present but this inference could not be proved by removing the cellulose owing to the violence of the sulphuric acid reaction. The extremely thin tylosic wall ruptured long before the xylary cells became dissociated. The cellulosic layer of the wall, in contrast, was sufficiently strong to permit the tylosis to remain intact after complete delignification and appeared to exist as a continuous strip of cellulose rather than of small irregular patches of this substance.

2. The tyloses of Type A2 were similar in all respects to those of Type A1 except that an inner layer of lignin was observable in the tylosic wall while the sections were undergoing treatment.

3. The tyloses of Type B were identical to those of Isenberg's Class 3. The layers of lignin in the tylosic wall bounding the cellulosic layer within and without were clearly discernible in sections swollen with cellulose solvents. The cellulose layer occupied the bulk of the cross-sectional area of the wall.

4. The sclerosed tyloses of Type C with stratified walls were dissimilar to any of the classes listed by Isenberg. All of the wall layers, with the exception of the middle lamella, appeared to be crystalline, that is, cellulosic, throughout. An external (third) layer of lignin was not evident at any time. The thick secondary layer of the wall dissolved rapidly both in 72 per cent H_2SO_4 and Schweizer's Reagent, indicating, particularly in the latter instance, its cellulosic nature.

SUMMARY AND CONCLUSIONS

1. Tyloses are more abundant and a more constant feature in white oaks than in red oaks, but the two subgenera cannot be distinguished with certainty on the basis of the presence or absence of these structures.

2. In general, tyloses in *Leucobalanus* are different structurally from those in *Erythrobalanus*. In white oaks, the tyloses possess walls averaging 3–5 microns in thickness, as a rule, and are moderately abundant; in comparison, two major morphological types of tyloses can be recognized in red oaks, namely, (a) those with walls under 2 microns in thickness, that are abundant or even crowded (Type A2 of table 1) and (b) sclerosed tyloses with walls averaging 5–50 microns in thickness that are frequently stratified and pitted as well, such tyloses ranging from sparse to abundant. (Type C. table 1.)

3. Exceptions to the situation stated under 2 occur but they are not frequent. An intermediate type of tylosis occurs in two species of each subgenus (*Q. montana* Willd., and *Q. bicolor* Willd. in *Leucobalanus; Q. ellipsoidalis* Hill and *Q. kelloggii* Newb. in *Erythrobalanus*) in which the wall is under 2 microns in thickness and the tylosic number is low (Type A1, table 1). Further, two red oaks (*Q. marilandica* Muench. and *Q. cinerea* Michx.) exhibit tyloses of the white oak type throughout the heartwood. The predominant type of tylosis present in all other *Quercus* species conforms to 2.

4. The structural variation of tyloses reaches a peak in *Erythrobalanus;* on the basis of tylosic type and abundance, several subdivisions, each embracing a number of species, can be recognized (see tables 1 and 3).

5. The white oaks, in contrast to the red, do not lend themselves to ready subdivision into groups of species on the basis of the varying morphological nature or abundance of tyloses. Several chestnut oaks appear to be an exception to this rule but since the tylosic features of this group of species exhibit no uniformity, definite deductions cannot be made.

6. The chemical composition of tylosic walls in *Quercus* is more complex than is indicated by the work of Isenberg (op. cit., p. 9). Two distinct types can be recognized, viz:

(a) tyloses with from thin to moderately thick walls (under 5 microns), the latter composed of a central cellulosic layer with thin layers of lignin on its flanks.

(b) tyloses with thick (over 5 microns) and stratified walls which frequently possess pits, the wall composed of a lignified inner layer (middle lamella) followed centripetally by a cellulosic layer, with no layer of lignin to the inside.

7. The physical nature of the tylosic content of *Quercus* woods, occasioned in turn by variations in the wall thickness of tyloses and the number of these per unit of volume, that is, by their size, are more readily decipherable and can be used with much greater ease than the chemical distinctions enumerated in the latter part of this paper.

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BULLETIN OF THE TORREY BOTANICAL CLUB
69(1): 11–20 JANUARY, 1942

THIAMIN CONTENT OF AGAR[1]

DOROTHY DAY

INTRODUCTION

The need for a careful study of agar became obvious during the early stages of another problem. At that time excised roots of tomato, which require thiamin, appeared to grow fairly well in an agar-mineral-sugar medium regardless of the presence of added thiamin. The present report is concerned with the determination by means of the growth of *Phycomyces Blakesleeanus* of the approximate quantity of thiamin or its intermediates in various samples of commercial and purified agar as well as in some samples of filter paper and cheesecloth, materials frequently used in the preparation of culture media.

Agar-agar, so commonly used for solidifying liquid media for the cultivation of micro-organisms, is prepared by drying a hot-water extract of certain marine algae. Because of its origin and the method of preparation it might be expected to contain some of the various growth substances originally present in the algae and perhaps some produced by micro-organisms which might develop in the extract during its desiccation. We should expect also that the amount of the growth substances in various samples of commercial agar would differ, depending upon how much they had been purified by washing or other treatments, and upon the character of any additions which might be made in preparing them for the market.

The presence of thiamin, of biotin, and of unidentified growth substances in commercial agar has been previously reported. Allison and Hoover (1934), using *Bacillus radicicola* as the test organism, detected the presence of Coenzyme R in agar. Coenzyme R was later demonstrated by György and his coworkers (1940) to be identical with biotin or vitamin H. Hawker (1936) found that a scanty growth of *Melanospora destruens* developed on a mineral-glucose medium containing 1.5 per cent agar. No growth occurred in the medium without the agar. These observations were interpreted as indicating the presence of traces of the second of two factors which must be present for the development of this organism. The second factor was later demonstrated to be biotin (1939).

Fries (1938) reported that *Polyporus abietinus* and *Polyporus adustus* grew and formed aerial mycelium on a mineral-sugar medium containing

[1] Contributions from the Department of Botany, Smith College, New Series, No. 8.
I am indebted for many courtesies to the staff of the New York Botanical Garden, where these experiments were performed.

ammonium nitrate and 1.5 per cent agar. Since both of these organisms are thiamin-deficient and do not grow in a liquid medium lacking thiamin, or its pyrimidine intermediate, growth on the agar medium may be taken as prima facie evidence for the presence of thiamin in the agar. Fries observed further that the growth of these two organisms was much less on a medium containing washed agar than on one containing unwashed agar. The washed agar was prepared by extracting discs of 3.0 per cent agar with two changes of distilled water during a 24-hour period.

Fromageot and Tchang (1938) observed that *Rhodotorula Sannei* grew on a mineral-sugar medium containing 2.0 per cent washed agar but failed to grow in the same medium without the agar. This organism does not grow without thiamin or its intermediates in the medium. Their observations indicate that their washed agar contained thiamin or pyrimidine.

Robbins (1939) reported the presence in agar of thiamin or its intermediates as determined by the growth of *Phycomyces Blakesleeanus*. Evidence for the presence of unidentified growth substances (Factor Z) in agar was presented by Robbins (1941a). Robbins (1941b) and Robbins and Ma (1941) found as much as 0.1 mμ mole of biotin per gram in some samples of agar; the biotin was determined by the growth of *Ashbya Gossypii*.

Schopfer and Rytz (1938) found appreciable quantities of thiamin or its intermediates in crude cotton as judged by the growth of *Phycomyces* but little or none in white, bleached cotton.

The literature cited indicates that various growth substances may be present in agar in sufficient amounts to be significant in determining the growth of micro-organisms. However, agar may influence growth for other reasons than its growth-substance content. Its ash, especially the trace elements, may be important for some organisms and under some conditions (Leonian and Lilly, 1940). Rippel (1936) found the colloidal character of the agar significant in favorably affecting the growth of *Azotobacter* and *Aspergillus niger*. Other reasons have been suggested why agar should affect growth, but no attempt will be made here to review such possibilities in detail.

METHODS AND MATERIALS

Phycomyces Blakesleeanus (+) strain was grown at 25° C. on 25 ml. of medium in 125 ml. Erlenmeyer flasks of Pyrex glass cleaned with chromic acid cleaning solution and thoroughly rinsed with tap water and distilled water. The media were sterilized at 15 lb. pressure for 20 minutes. For inoculum several sporangia were broken in a flask containing 25 ml. of sterile distilled water; one drop of this suspension was added to each flask of the medium to be tested. All cultures were grown in quadruplicate.

The basal medium contained per liter of distilled water: 1.5 g. KH_2PO_4, 0.5 g. $MgSO_4 \cdot 7\ H_2O$, 50.0 g. dextrose, 2.0 g. asparagine, and mineral supple-

ments in p.p.m. as follows: B 0.005, Cu 0.02, Fe 0.10, Ga 0.01, Mn 0.01, Mo 0.01, Zn 0.09. The commercial asparagine was purified by treatment with Norit A and recrystallization from alcohol. The thiamin was Merck's synthetic betabion; the pyrimidine was 2-methyl-5-bromomethyl-6-aminopyrimidine dihydrobromide. The amount of thiamin or its intermediates is expressed in millimicromoles (mμ moles).

The agars were Difco granulated bacto-agar, Eimer and Amend agar-agar flakes, and crude, shred agar. For parts of some experiments the granulated and flake agars were thoroughly leached with 5.0 per cent aqueous pyridine, with distilled water, and with alcohol, boiled with alcohol, and dried; these are referred to as "purified agars." The leachings and washings obtained from a particular agar were freed of pyridine and alcohol and concentrated by evaporation on a hot plate; these are referred to as "agar extracts." A portion of the shred agar was electrodialyzed.

Filter paper of two types was also used; one was a low grade paper, No. 613, from Eaton and Dikeman, while the other was "Genuine" Whatman "ashless." These were cut in pieces about one inch square and boiled in distilled water for 20 minutes. The liquid was drained from the paper and concentrated by evaporation on a hot plate. Two samples of cloth, commonly known as "cheesecloth" and as "tobacco cloth" respectively, were treated similarly. These liquids are referred to as paper and cloth extracts.

The several kinds of agar, of purified agars, of corresponding agar extracts, of paper extracts, and of cloth extracts were added to the basal medium in various proportions and combinations. In every experiment several portions of each type of medium were supplemented by the addition of small known amounts of thiamin.

At the end of one week observations were recorded on the growth of mycelium and appearance of sporangia. Dry weights of the mycelium in the flasks were determined as follows: Each flask was filled with hot distilled water and placed on a hot plate until the agar melted. The mycelium was then fished from the flask, washed in boiling distilled water, dried at 95–100° C. for 18–24 hours and weighed.[2]

THIAMIN CONTENT OF VARIOUS COMMERCIAL AGARS

In the basal culture medium growth of *Phycomyces* was lacking or negligible. The addition of thiamin to this medium resulted in abundant growth of *Phycomyces*.

Thiamin in Difco Granulated Agar. When the basal medium was solidified with Difco agar, lot 318721, in each test in which 0.5 or 1.0 g. agar

[2] A comparison of the dry weight of untreated mycelium of *Phycomyces* grown in liquid culture containing thiamin with the dry weight of mycelium which had been boiled and washed before drying showed the latter to be 12–15 per cent lower.

per flask was used, *Phycomyces* formed mycelium with sporangia in all four flasks (fig. 1). The dry weight was roughtly proportional to the amount of agar in the flask; for example, in experiment 16 (see table 1) the dry weight was 28.8 mg. with 1.0 g. agar, 13.9 mg. with 0.5 g. agar, 7.9 mg. with 0.25 g. agar, and 6.2 mg. with 0.125 g. agar. This growth of *Phycomyces* when agar was added to the basal medium indicated the presence in this agar of thiamin or its intermediates. From the relation between the amount of thiamin and the dry weight of *Phycomyces* grown in liquid culture it was calculated that the agar contained about 0.1 mμ mole thiamin per gram.

The most obvious differences in five tests of this agar were in experiments 10 and 11, in which the dry weights ranged from 19.0 mg. to 34.4 mg., or an indicated 0.07–0.16 mμ mole thiamin, per 1.0 g. agar. In one experiment, 29, with 1.0 g. and 0.5 g. agar the dry weights were 29.3 mg. and 17.5 mg. respectively for lot 318721, 24.9 mg. and 10.6 mg. for 325120, and 14.6 mg. and 8.8 mg. for 332408. In terms of equivalent amounts of thiamin the first two lots of agar contained about 0.1 mμ mole and the third lot less than one-half this amount. The variations in these results may be due to one or more of

TABLE 1

*Growth of Phycomyces Blakesleeanus on agars and on agar extracts. All cultures contained the same amounts of mineral salts, dextrose and asparagine. Dry weight is recorded in mg. per culture.**

Experiment number	Untreated agar		Purified agar		Agar extract from	
	1.0 g.	0.5 g.	1.0 g.	0.5 g.	1.0 g.	0.5 g.
	Difco granulated agar, Lot #318721					
10	19.0	12.2	0.5	1.3	.....	.....
11	25.5	.....	0.5	.....	11.2	9.9
11	34.4	.....	.....	.....	.....	.....
13	28.4	16.7	.....	0.2	12.1	7.6
16	28.8	13.9	0.2	0.2	.....	.....
16	27.9	.....	1.0	.....	.....	.....
29	29.3	17.5	.....	.....	.....	.....
Average	27.6	15.1	0.5	0.6	11.6	8.8
General average per 1.0 g.	28.9		0.9		14.6	
	Eimer and Amend flake agar					
11	2.2	.....	.....	.....	.....	.....
12	3.9	3.2	1.5	1.8	.....	.....
13	1.9	0.3	0.5	0.4	.....	.....
15	.....	.....	.....	.....	12.0	3.3
15	.....	.....	.....	.....	11.3	16.9
16	3.1	2.1	0.3	0.7	.....	.....
16	3.5	.....	0.8	.....	.....	.....
Average	2.9	1.9	0.8	1.0	11.7	10.1
General average per 1.0 g.	3.4		1.4		16.0	

* Since the results presented here were confirmed by tests with flasks containing 0.25 g. and 0.125 g. agar, the latter data are not included in this table although they are occasionally cited in the body of the paper.

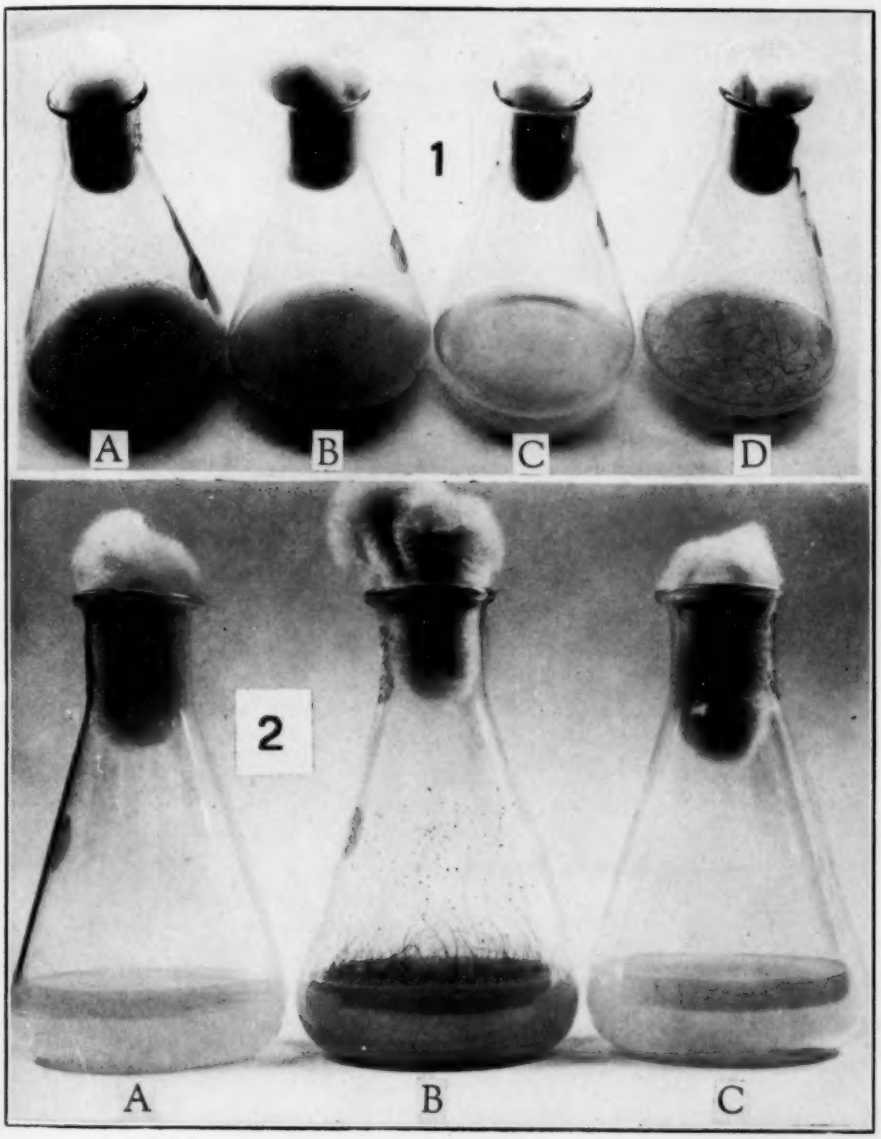

FIG. 1. Effect of different amounts of agar on growth of *Phycomyces*. Each flask contained 25 ml. of the same basal medium plus: A, 1.0 g. Difco agar; B, 0.5 g.; C, 0.125 g.; D, 0.125 g. agar and 0.1 mμ mole thiamin. Age 7 days. The darker appearance of the material in A (the flask on the left) is due to the larger amount of agar in the medium as well as to greater growth of mycelium with numerous sporangia. FIG. 2. Effect of different kinds of agar on growth of *Phycomyces*. Each flask contained 50 ml. of the same basal medium plus 1.0 g. agar; A, purified Difco agar; B, untreated Difco agar; C, untreated Eimer and Amend agar. Age 7 days. The darker appearance of the material in the middle flask is due to the substances in the untreated Difco agar as well as to the greater growth of mycelium with sporangia.

several causes, such as loss of mycelium in taking it from the flask, incomplete removal of the agar from the mycelium, unequal inoculation of the flasks in different experiments, or to some other factor. The lesser dry weight in the third lot of agar may indicate a difference in the amount of thiamin in separate lots of agar.

A known amount of thiamin added to a definite quantity of agar in the basal medium gave about 64 per cent of the dry weight that would be expected by adding that on liquid culture with added thiamin to that on the basal medium with agar; for example, addition to 1.0 g. agar of 0.05 mμ mole thiamin gave 31.4 mg. in place of the expected 45.0 mg., and of 0.5 mμ mole thiamin, 57.2 mg. in place of 100 mg. This may be due to some unexplained error, or it may indicate that the dry weight produced in an agar medium with added thiamin is less than that in a liquid medium with the same amount of thiamin. If this is true, the thiamin content of agar is more than is indicated by the figures mentioned, for all calculations of the probable amounts of thiamin were made on the relation between thiamin and dry weight of mycelium produced in liquid cultures.

Thiamin in Eimer and Amend flake agar. This agar produced sparse mycelium with few or no sporangia (fig. 2). Although greater dry weight usually was obtained in the presence of more agar the proportion was not definite, as it was with Difco agar; for example, in experiment 13 the resulting dry weights were 1.9 mg., 0.3 mg., 1.8 mg., and 1.2 mg. for 1.0 g., 0.5 g., 0.25 g., and 0.125 g. agar respectively. The very small dry weights average only 2.9 mg. with 1.0 g. agar (table 1), or less than 0.01 mμ mole thiamin. This amount was scarcely one-tenth of that found in Difco agar. Here, also, the addition of a known 0.5 mμ mole thiamin to 1.0 g. agar gave dry weight of about 60 per cent of what might have been expected.

Thiamin in crude, shred agar. This agar contained some thiamin. The dry weight was 5.3 mg. for 0.25 g. agar and 3.2 mg. with 0.125 g. agar, a response roughly proportional to the quantity of agar in the flask. The thiamin indicated was about 0.09 mμ mole in one gram of agar, an amount midway between those in the two other types of agar.

Because *Phycomyces Blakesleeanus* did not grow in a liquid medium but grew in the same medium when it was supplemented by a known quantity of agar, it would appear that commercial agar contains thiamin or its intermediates. Difco granulated agar contained more of this vitamin than did a crude, shred agar which in turn had more than the sample of Eimer and Amend flake agar used.

EFFECT OF THE PURIFICATION OF AGAR ON ITS THIAMIN CONTENT

Samples of Difco granulated agar and of Eimer and Amend flake agar were purified with pyridine and were then used to solidify the basal medium.

In all of the tests with purified agars *Phycomyces* formed only sparse mycelium and sporangia were generally absent or very rare (fig. 2). When thiamin was introduced into the medium with either of the purified agars, growth was prompt and definite. This indicated that the sparse growth of *Phycomyces* in the purified agar media was due to a lack of thiamin and not to toxicity of the purified agar caused by a residuum of pyridine or other causes.

With purified Difco agar, lot 318721, the dry weight of *Phycomyces* was never more than 3.6 mg. per 1.0 g. agar (table 1). The dry weight was not proportional to the amount of agar present; for example, in experiment 10 the dry weights were 0.5 mg., 1.3 mg., 0.9 mg., and 1.2 mg. with 1.0 g., 0.5 g., 0.25 g., and 0.125 g. agar respectively. This indicated considerably less than 0.01 mμ mole thiamin per 1.0 g. purified Difco agar, or less than one-tenth the amount present before the treatment with pyridine. The addition to 1.0 g. purified agar of 0.05 mμ mole thiamin gave 20 per cent of the anticipated dry weight and of 0.5 mμ mole gave 66 per cent of the expected weight. Added to 0.125 g. agar these same amounts of thiamin gave 30 per cent and 60 per cent, respectively, of the anticipated dry weights.

With purified Eimer and Amend agar the general average for the dry weight per gram of agar was 1.4 mg.; however individual determinations varied considerably (table 1). The dry weights were not proportional to the amount of purified agar; for example, in experiment 13 the dry weights were 0.5 mg., 0.4 mg., 2.3 mg., and 1.3 mg. with 1.0 g., 0.5 g., 0.25 g., and 0.125 g. agar respectively. This was equivalent to somewhat less than 0.01 mμ mole thiamin in 1.0 g. purified Eimer and Amend agar, possibly one-half the amount present before extraction. The addition of 0.5 mμ mole thiamin to 0.5 g. purified Eimer and Amend agar gave dry weight of 31.7 mg. in place of the calculated 84.0 mg., to 0.125 g. agar, 3.3 mg. in place of 19.0 mg.

Crude shred agar subjected to electrodialysis formed scanty mycelium with dry weights of 2.6 mg. and 1.0 mg. per 0.25 g. and 0.125 g. agar respectively. The relation between the dry weight of *Phycomyces* and the amount of agar was closer than it was for either of the two types of agar purified with pyridine. The amount of thiamin indicated was approximately 0.02 mμ mole, or about one-fourth the amount present in the shred agar before electrodialysis and about twice as much as in the two agars purified by pyridine.

From these results it would appear that thiamin was largely or completely removed from agar by leaching with pyridine. Electrodialysis also removed thiamin from agar but was somewhat less effective than leaching with pyridine. Several tests, not reported here in detail, indicated that washing agar in distilled water removed some thiamin, but further study is needed to determine whether leaching with water is as satisfactory as with pyridine.

THIAMIN IN AGAR EXTRACTS

The agar extracts were added to the basal medium in amounts equivalent to the quantities of agar used in the earlier tests. Growth of *Phycomyces* on each of these agar extracts was superior to that on either of the purified agars.

The dry weights with Difco agar extract averaged 11.6 mg. for the extract of 1.0 g. agar and 8.8 mg. for 0.5 g. agar (table 1). The general average for the equivalent of 1.0 g. agar was 14.6 mg., or about 0.04 mμ mole thiamin, not quite one-half the amount in this same lot of untreated agar.

With Eimer and Amend agar the dry weights averaged 11.7 mg. and 10.1 mg. for the extract of 1.0 g. and 0.5 g. agar respectively (table 1). The general average for the equivalent of 1.0 g. agar was 16.0 mg., or 0.05 mμ mole thiamin, which was about five times as much as was found in the original Eimer and Amend agar.

These differences between the thiamin content of the extract and the original agar are difficult to understand. Aside from the possibility of experimental error, which I do not believe is responsible, the following possibilities should be considered: Some thiamin may have been destroyed in the process of concentrating the agar extract under alkaline conditions created by the presence of pyridine. This would account for the smaller amount of thiamin found in the extract of the Difco agar as compared to the original agar. The more rapid percolation of the aqueous pyridine through the Eimer and Amend flake agar allowed periods when little liquid was present and the agar mass was moist and well aerated. This may have permitted the development of micro-organisms which increased the thiamin content of the extract beyond that of the original agar. The validity of these suggestions has not been determined, but they are offered as possible explanations.

When Difco agar extract was added to an equivalent amount of purified Difco agar in the basal medium, this combination gave dry weights of 2.8 mg., 2.0 mg., 2.2 mg., and 2.0 mg. for 1.0 g., 0.5 g., 0.25 g., and 0.125 g. respectively. With Eimer and Amend agar a similar combination of purified agar plus agar extract gave 1.9 mg., 0.7 mg., and 1.3 mg. for 0.5 g., 0.25 g., and 0.125 g. respectively. A comparison of these figures with those noted earlier shows that growth of *Phycomyces* was much less here than on the untreated agar, was less than on the agar extract, was less than on purified agar with 0.05–0.5 mμ mole added thiamin, and was little more than on the purified agar; this was true for both the Difco and the Eimer and Amend agars and their extracts. These results confirmed and emphasized the point suggested in the earlier data that changes may have taken place during the process of leaching the agar, changes which were more than the simple washing out

of thiamin. Whatever the causes may be, it is obvious that purified agar plus agar extract is not equivalent to the original, untreated, commercial agar.

WATER EXTRACTS FROM FILTER PAPER AND CLOTH

Growth of *Phycomyces* with extracts from filter paper indicated less than 0.01 mμ mole thiamin per 1.0 g. Eaton and Dikeman paper and almost 0.02 mμ mole thiamin for 1.0 g. Whatman paper. Similar tests indicated about 0.03 mμ mole thiamin per 1.0 g. cheesecloth and about 0.15 mμ mole thiamin per 1.0 g. tobacco cloth. While these amounts of thiamin in filter paper and cheesecloth may seem small, especially those from the filter paper, they are definite and are large enough to cause a serious experimental error if the presence of thiamin were not realized.

DISCUSSION

Although a high degree of accuracy cannot be claimed for experiments in which the growth substances occur in such minute amounts as they did in the materials which were used, demonstration of a measurable quantity of thiamin[3] in commercial agar, in cheesecloth, and in filter paper emphasizes the need for care in laboratory procedure in which growth substances are involved. Proper precautions are especially important, because growth substances are active in minute amounts such as may be present in agar or obtained from filter paper or cheesecloth used in the laboratory.

Purification of agar with five per cent aqueous pyridine appeared satisfactory, but other methods, such as washing with water, may prove as effective and simpler for the removal of thiamin.

The dry weight of *Phycomyces* on agar media to which thiamin was added and on purified agar to which agar extract was added was less than anticipated from growth of this organism in liquid cultures in the presence of known quantities of thiamin. These observations raise the question whether the response of *Phycomyces* to a given quantity of thiamin may not be greater in a liquid medium than in an agar medium because of lessened availability of thiamin in the presence of agar, because of decreased supply of water or another essential substance, or because of some other factor.

SUMMARY

1. *Phycomyces Blakesleeanus* grew better and produced greater dry weight in a medium solidified with Difco agar or with Eimer and Amend agar than it did in the same medium without the agar. Because the basal medium contained minerals, sugar and asparagine but no added thiamin, this result was interpreted as indicating the presence of thiamin or its

[3] It should be pointed out that this study is concerned not only with thiamin as such but also with the thiazole and pyrimidine intermediates to which also *Phycomyces* responds.

intermediates in these agars. Different kinds of agar varied in thiamin content.

2. Thiamin was largely or completely removed by leaching the agar with five per cent aqueous pyridine, as was shown by lack of growth of *Phycomyces* in purified agars and by its growth in the agar extracts. Electrodialysis proved no more efficient in purifying agar than washing with five per cent pyridine.

3. Cheesecloth, tobacco cloth and filter paper also were found to contain appreciable quantities of thiamin as measured by the growth of *Phycomyces*.

4. Washing agar, filter paper and cheesecloth with distilled water removed some of the thiamin.

5. Demonstration of thiamin in these frequently used materials emphasized the need for care in laboratory technique.

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BULLETIN OF THE TORREY BOTANICAL CLUB
69(1): 21–26 JANUARY, 1942

THE EFFECT OF ACTINOMYCES ALBUS AND OF THIAMIN ON THE GROWTH OF TRICHOPHYTON DISCOIDES

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INTRODUCTION

The fungus *Trichophyton discoides* Sabouraud is a common cause of tinea in calves in Uruguay. It is also a frequent cause of tinea of the scalp, the beard, and the glabrous skin of man. These infections are usually very inflammatory. On Sabouraud's media, *T. discoides* grows slowly and produces a flat, smooth, and usually glabrous giant colony; some strains produce a central umbo and short velvet; the colony has a brownish neutral color. Sabouraud (5) did not describe conidia; but in 1934 Lebasque (2) observed aleurospora and closterospora in cultures on different cereals and on horse dung. Cazalbou (1) describes phases in the cultures of *T. discoides;* where *T. discoides* is mentioned in this paper the so-called normal phase is to be understood.

During study of our strain 688, a culture on glucose-peptone agar was accidentally contaminated by an *Actinomyces* of the *Actinomyces albus* group. *A. albus* (strain 693) began to grow at a distance of four cm. from a colony of *T. discoides*. After 15 days the sector of the colony of *T. discoides* nearest to the colony of *A. albus* became folded and velvety while the other sectors remained smooth and glabrous. Folding of the colony was due to an increase of the growth. The fact was confirmed many times (fig. 1). If the agar between the two colonies was cut, the *Actinomyces* had no further influence over the growth of the *Trichophyton*.

The same results were obtained with another strain of the *Actinomyces albus* group, isolated from the soil (strain 800). A successful attempt was made also to increase the growth of another strain of *T. discoides* (strain 461).

These experiments proved that our strains of *Actinomyces albus* have a beneficial effect on the growth of *T. discoides* and that this effect is produced by a water-soluble substance. The importance of thiamin for plant growth has been recently emphasized by Robbins (3). In the thought that perhaps thiamin was the cause of the increase in the growth of *T. discoides*, the following experiments were made.

EXPERIMENTS WITH GLUCOSE-PEPTONE AGAR

The culture medium was made up as follows: bacto-peptone 10 g., pure Grübler glucose 40 g., agar 20 g., distilled water 1 l. Approximately 100

ml. of this medium was poured in flasks with a flat side 19 cm. long and 5.5 cm. wide. Six flasks were arranged in three groups of two each. The thiamin chloride used was the synthetic crystalline product of Roche called "Aneurine."

To the flasks of the first group nothing was added. To each flask of the second group the mycelium of three cultures of *A. albus*, also on glucose-peptone agar, was added; these cultures had been incubated 15 days at 37° C. To the flasks of the third group 0.5 ml. of a 1:10,000 thiamin solution was added. The six flasks were heated at 100° C. for 30 minutes and then placed on their sides until the medium solidified. The layer of agar was 1 cm. thick.

The six flasks were inoculated with *T. discoides* in order to obtain giant colonies, and kept for 20 days in the incubator at 37° C. After this period the colonies which were growing on glucose-peptone agar (first group of flasks) were flat, smooth, and glabrous; they had produced a scanty mycelium and were from 4.5 to 5 cm. in diameter (fig. 2). The colonies in the flasks of the second group, with mycelium of *A. albus*, were folded and covered with a short velvet; they had produced abundant mycelial growth (fig. 3). The colonies in the flasks of the third group, with thiamin, were even more folded and velvety; they were from 3.5 to 4.5 cm. in diameter (fig. 4).

Aleurospora and closterospora were produced by the colonies in the flasks with mycelium of *A. albus* or thiamin, but were very scarce. *T. discoides*, when cultivated in media with thiamin or mycelium of *A. albus*, grows only over the surface of the agar; but when cultivated on media to which thiamin or *A. albus* had not been added, it produces a scanty growth over the surface and also submersed mycelium.

I inoculated peptone-glucose agar with mycelium of the folded, velvety colonies, which were growing in the medium with thiamin, and obtained again flat, smooth, glabrous colonies.

These experiments demonstrate that *Actinomyces albus* elaborates a thermostable and water-soluble substance which has an effect on the growth of *T. discoides* similar to that of thiamin.

EXPERIMENTS WITH SYNTHETIC MEDIA

The following experiments were undertaken to determine if *Actinomyces albus* is really autotrophic for thiamin. The researches of Schopfer and of Robbins have demonstrated that *Phycomyces Blakesleeanus* Burgeff requires thiamin and that it is unable to synthesize this growth substance from sugar, asparagine, and minerals; this fungus produces a mycelial mat and sporangiophores only when supplied with thiamin or with both its intermediates, thiazole and pyrimidine.

P. Blakesleeanus was grown in a medium similar to that used by Robbins

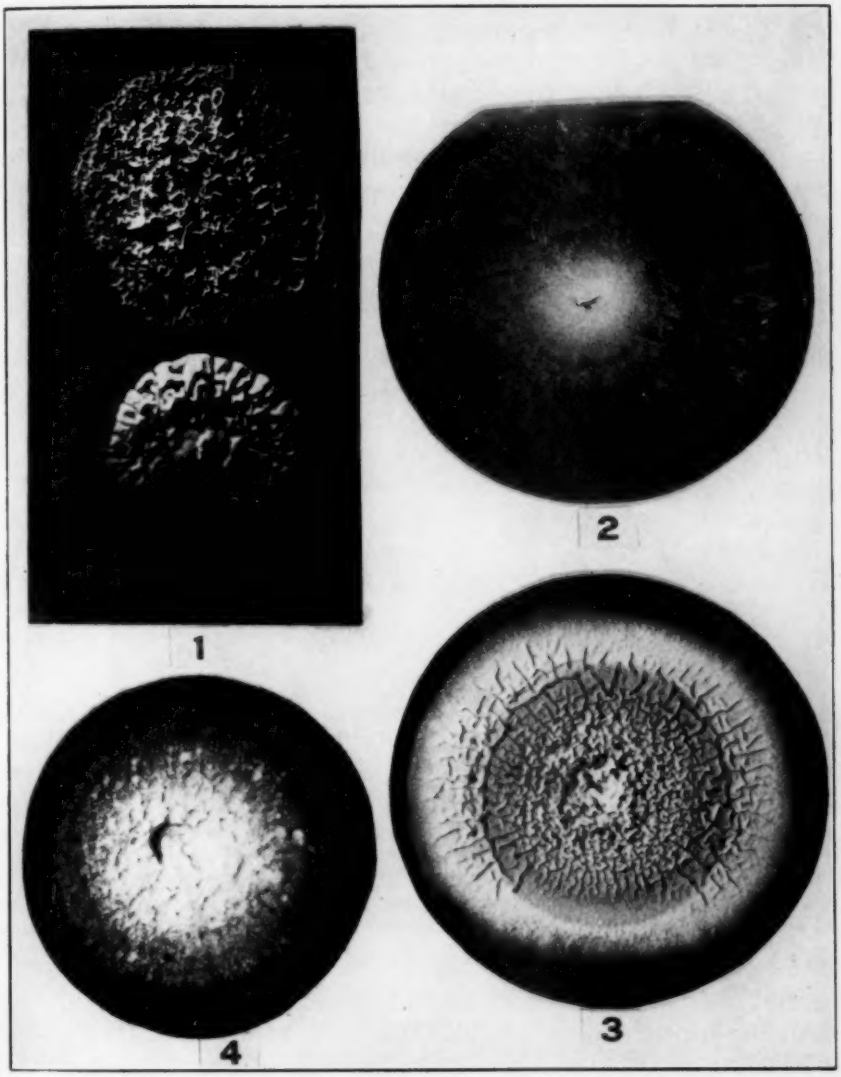

FIG. 1. *Actinomyces albus* (above) and *Trichophyton discoides* (below) growing in the same flask. *A. albus* benefits the growth of the upper part of the colony of *T. discoides*. FIG. 2. *Trichophyton discoides* (strain 688). Giant colony aged 20 days growing on glucose bacto-peptone agar. ×1. FIG. 3. *Trichophyton discoides* (strain 688). Giant colony aged 20 days growing on glucose bacto-peptone agar plus mycelium of *Actinomyces albus*. ×1. FIG. 4. *Trichophyton discoides* (strain 688). Giant colony aged 20 days growing on glucose bacto-peptone agar plus thiamin. ×1.

(4), its composition being: dextrose 100 g., asparagine 1.0 g., $MgSO_4 \cdot 7H_2O$ 0.5 g., KH_2PO_4 1.5 g., bacto-agar 10 g., redistilled water 1 l. To this medium 0.1 ml. of the following solution of mineral supplements was added: H_3BO_3 5.7 mg., $CuSO_4 \cdot 5H_2O$ 18.6 mg., $(NH_4)_2Fe_2(SO_4)_4 \cdot 24H_2O$ 173 mg., $MnCl_2 \cdot 4H_2O$ 7.1 mg., ammonium molybdate (85 per cent) 3.6 mg., $ZnSO_4 \cdot 7H_2O$ 79 mg., redistilled water 100 ml. The medium was poured in 250 ml. Erlenmeyer flasks of Murano glass, 40 ml. in each flask. The flasks were arranged in three groups.

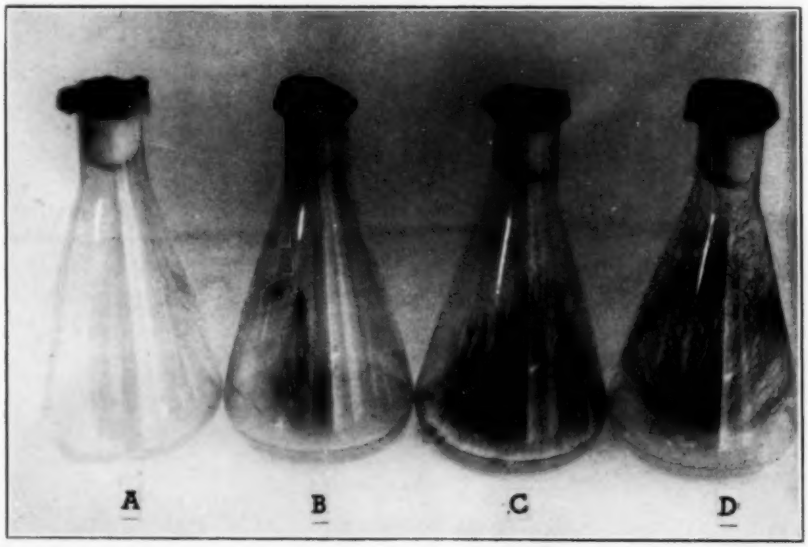

FIG. 5. Elaboration of thiamin by our strain 800 of the *Actinomyces albus* group tested by the growth of *Phycomyces Blakesleeanus*. From left to right: A. Culture on a medium lacking thiamin; no sporangiophores. B. On the same medium plus filtered cultures of *Actinomyces albus;* few sporangiophores. C. On the same medium plus mycelium of *A. albus;* luxuriant growth constituted mainly by a huge number of sporangiophores. D. On the same medium plus thiamin.

Group 1. To two flasks were added 10 ml. of Czapek medium of the following composition: $NaNO_3$ 2 g., K_2HPO_4 1.0 g., $MgSO_4 \cdot 7H_2O$ 0.5 g., KCl 0.5 g., $FeSO_4 \cdot 7H_2O$ 0.01 g., dextrose 40 g., bacto-agar 20 g., redistilled water 1 l. The media were melted and then mixed. After solidification of the medium the two flasks were inoculated with mycelium of *Phycomyces Blakesleeanus,* the plus strain. After 10 days at a temperature between 15° and 20° C., a scanty, sparse mycelial growth was evident; no sporangiophores were produced (fig. 5 A).

Group 2. To two flasks were added 10 ml. of Czapek medium and four drops of 1:10,000 thiamin solution. *P. Blakesleeanus* developed fairly well; long sporangiophores and a mycelial mat were produced (fig. 5 D).

Group 3. To four flasks were added 10 ml. of cultures of *Actinomyces albus* (strain 800) on Czapek medium. These cultures had been incubated at 37° C. for 15 days. After it had been heated at 100° C., *A. albus* died. *P. Blakesleeanus* grew in these flasks as well as in the flasks with thiamin (fig. 5 C).

A. albus was grown also in Czapek liquid medium. After 15 days the culture was filtered through a Berkefeld filter and the extract was added to the agar which lacked thiamin. In this medium only a few sporangiophores were produced (fig. 5 B).

The experiments demonstrate that our strain 800, of the *A. albus* group, is autotrophic for thiamin.

OTHER EXPERIMENTS

Growth of Phycomyces Blakesleeanus on glucose-peptone agar: This fungus grew well on this medium; but the addition of from 0.00005 to 0.0001 g. thiamin to 100 ml. of the medium produced a great increase in growth. This experiment seems to show that our medium (Sabouraud's formula) has an insufficient quantity of thiamin or of one or both intermediates.

Cultures of Trichophyton discoides on synthetic media: I was unable to cultivate *T. discoides* on the two media referred to above. The addition of thiamin to such media did not modify this result.

An inhibitory effect of A. albus over P. Blakesleeanus: Glucose peptone agar was inoculated with our strain 693 of *A. albus* in order to have a few colonies. Six days later we inoculated the same flasks, where *A. albus* was already growing, with mycelium of *P. Blakesleeanus.* We observed that the growth of *Phycomyces* was increased near the colonies of *A. albus;* but very close to the colonies (1 mm.) the mycelium of the *Phycomyces* ceased growth.

DISCUSSION

The above experiments indicate that our strains of *Actinomyces albus* are autotrophic for thiamin, since their mycelium permits *Phycomyces Blakesleeanus* to produce a luxuriant growth and long sporangiophores in media which lacked thiamin. No information was furnished of interest in the physiology of *Trichophyton discoides;* our experiments only demonstrate that thiamin benefits its growth on media prepared with bacto-peptone.

In medical mycology the identification of species is frequently made by the aspect of the giant colonies. The colony growth of *T. discoides* may vary greatly with the addition of small amounts of thiamin. The culture media are not always prepared with the same products, and one must therefore be cautious not to attach too much importance to small differences between the descriptions and figures of different authors. Many such small differences in

the aspect of the giant colonies have been considered as deserving specific rank.

SUMMARY

Strains of actinomyces, of the *Actinomyces albus* group, have a stimulating influence over the growth of *Trichophyton discoides* Sabouraud, when the latter is grown on glucose bacto-peptone agar. The giant colonies, usually flat, smooth, and glabrous, become folded and velvety.

The addition of thiamin to the glucose bacto-peptone agar has the same effect as *A. albus* on the growth of *T. discoides*.

An agar medium lacking thiamin to which cultures of *A. albus* on glucose Czapek medium have been added permits *Phycomyces Blakesleeanus* to produce long sporangiophores as well as if thiamin had been added. Filtered cultures of *Actinomyces albus* in liquid Czapek medium have a similar but less marked effect.

The author is deeply indebted to William J. Robbins, Director of The New York Botanical Garden, for his advice and for the strain of *Phycomyces Blakesleeanus* that he kindly furnished us.

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BULLETIN OF THE TORREY BOTANICAL CLUB
69(1): 27–40 JANUARY, 1942

STUDIES IN THE CRASSULACEAE—III. SEDUM, SUBGENUS GORMANIA, SECTION EUGORMANIA[1]

ROBERT T. CLAUSEN

Generic limits in the Crassulaceae are indefinite. Probably there never will be agreement regarding the boundaries of the various genera. The group of species which Britton (1903) included in *Gormania* was originally characterized by the horizontal rootstocks, the petals united below the middle and somewhat spreading above, the stamens borne on the corolla and the carpels united below. Yet, if one surveys the genus *Sedum*, even denuded of the many generic segregates, there still remain species which possess one or the other of all characters indicated as diagnostic for *Gormania*. *S. spathulifolium* has the horizontal rootstocks, *S. adolphii* and *S. alsinefolium*, the petals united below the middle and the stamens borne on the corolla, and *S. fusiforme* the carpels united below. None of these characters is an absolute criterion for *Gormania*. Further, the statement about the petals must be modified somewhat. Study of fresh flowers indicates that there is considerable variation in the degree of fusion of the petals. They are only weakly united and can be pulled apart along the lines of fusion. Some of the species, referred by Britton to *Gormania*, now require somewhat different treatment. These include *Gormania debilis*, *G. oregana* and *G. anomala*. All three are morphologically intermediate between *Gormania* and *Sedum* in the strict sense. Cytological evidence indicates that the first is far removed from *Gormania*, while the floral structure of the last two divorces them from *Gormania* proper, but places them in related sections.

Cytological studies by Dr. Hollingshead (1942) suggest relationship of *Gormania* with the *Rosulata* of *Sedum*, also perhaps with the genus *Echeveria* which has been sampled by Baldwin (1939). The chromosomes are exceedingly small, elliptical or almost round, and rather numerous, either 30 or 90 in the diploid condition. These are illustrated in this issue in the paper by Hollingshead (1942). *S. debile*, treated as a *Gormania* by Britton, is $2n = 14–18$. Its chromosomes are larger and markedly 2-armed, quite different in shape from those of any species of *Gormania*. Cytologically it is closer to *S. divergens* ($2n = circa$ 16) which has two-armed chromosomes. *Sedum spathulifolium* of the section *Rosulata*, generally acknowledged as properly a

[1] This investigation was carried on with the aid of a grant from the Penrose Fund of the American Philosophical Society and a grant from the Trustee-Faculty Committee on Research of Cornell University. The cytological data are the result of studies by Dr. Lillian Hollingshead.

part of *Sedum*, is cytologically similar to *Gormania*. The chromosomes are small and round and, in all plants studied, the diploid number is 30. Although the cytological evidence indicates that section *Rosulata* and *Gormania* are closely similar, the differences in floral structure, inflorescence and leaves are considerable. In *Rosulata* the petals are not connivent, but are more quickly spreading in rotate fashion; the inflorescence is a three-parted cyme, not a paniculate cyme; and the leaves of the rosettes are flatter and less leathery. On a basis of these three criteria, *Gormania anomala* Britton is clearly a member of the section *Rosulata*. Further, it is not specifically different from *S. spathulifolium*.

Sedum oreganum merits special attention. Although originally placed in *Gormania* by Britton, it differs markedly in certain details. The petals are narrowly lanceolate, long acuminate, and connivent for only one-eighth of their length. The sterile rosettes are on leafy stems, with the leaves not leathery after the fashion of *Gormania*. Instead, in texture and appearance, the leaves are more like those of *S. divergens*. Probably, *S. oreganum* belongs in a section by itself, Section **Oreganica,** n. sect. (sectio nov., petalis anguste lanceolatis, longe acuminatis, erectis sed paululum conniventibus; rosulis caulibus 2–10 cm. longis, foliis carnosis sed non coriaceis).

In order to show seeming natural relationships, *Gormania* may now be treated as a subgenus of *Sedum* comprising three sections. The first of these sections, here designated as *Eugormania*, in the union of the petals below, seems to be morphologically closest to *Echeveria*, while the other two sections are morphologically closer to *Eusedum*.

Subgenus **Gormania** (Britton) Clausen, stat. nov.

Gormania Britton, Bull. N. Y. Bot. Gard. **3**: 29. 1903. Named in honor of M. W. Gorman of Portland, Oregon. TYPE SPECIES: *Cotyledon oregonensis* Watson.

Characteristics of this subgenus are the horizontal rootstocks, the prominent sterile rosettes and the petals which are erect at base for 1/10 or more of their length. The chromosomes are small and more or less round, in a euploid series of $n = 15$.

KEY TO THE SECTIONS OF GORMANIA

A. Petals connivent or united for ½ or more of length, divergent above; sterile rosettes with the leaves thick and leathery, usually glaucous; inflorescence a paniculate cyme ..... 1. Section *Eugormania*

AA. Petals free from the base or united for ½ of length, erect or widely spreading above; leaves fleshy, but not leathery; inflorescence a 3-parted cyme, sometimes compound.

B. Petals erect at base for about 1/10 of length, then widely spreading; leaves green or gray, often glaucous ..... 2. Section *Rosulata*

BB. Petals erect throughout, united at base for ⅓ of length; leaves very fleshy, green suffused with red, never glaucous ..... 3. Section *Oreganica*

Section EUGORMANIA

This section is distinguished by the characters indicated in the above key. The type species is the same as for the subgenus.

In the discussion under the species and subspecies, names of herbaria are abbreviated as: Bailey Hortorium, Cornell University, BH; Department of Botany, Cornell University, CU; California Academy of Sciences, CAS; Gray Herbarium, Harvard University, GH; New York Botanical Garden, NY; Santa Barbara Museum, SBM; Stanford University, DS; U. S. National Herbarium, US; and Willamette University, WILLU. Besides the specimens in the herbaria listed above, I have also made a rapid survey of the material in the herbarium of the University of California at Berkeley.

KEY TO THE SPECIES OF EUGORMANIA

A. Inflorescence and upper part of stem glandular pubescent, strongly reflexed before flowering time; leaves of rosettes glandular-ciliate; petals yellow ..... 2. *Sedum glanduliferum*

AA. Inflorescence and upper part of stem glabrous, usually erect before flowering time; leaves of rosettes usually not ciliate; petals yellow, white or pink ..... B

B. Flowers yellow or pale yellow, sometimes fading to white or pink in age; inflorescence a paniculate cyme; leaves of rosettes 1–3 cm. long ..... 1. *Sedum obtusatum*

BB. Flowers white, creamy white or pink; inflorescence a dense paniculate or corymbose cyme; leaves of rosettes 1–4.5 cm. long.

C. Flowers white or creamy white; sepals ovate, 2–3 mm. long. 3. *Sedum oregonense*

CC. Flowers pink or pale pink, rarely white; sepals lanceolate or ovate, 2–5 mm. long ..... 4. *Sedum laxum*

1. SEDUM OBTUSATUM A. Gray.

From the other species of the Section *Eugormania*, *Sedum obtusatum* may be distinguished by the yellow flowers which are borne in a glabrous paniculate cyme. The species is nearest to *S. oregonense*, from which it is only doubtfully distinct in the northern part of its range. That species has creamy white flowers, a paniculate-cymose inflorescence which is broadest and densest above, and larger rosette leaves; also, so far as present investigations indicate, it is hexaploid.

Sedum obtusatum may be divided into a southern subspecies with small rosette leaves and bright red stems and a northern subspecies with larger leaves and stems which are only slightly red or pink. The southern element, including the type, is native in the Sierra Nevada, ranging north to the region of the Feather River (fig. 1). The other race has its center of distribution in the southern Cascade Mountains. The two subspecies are separated in the following key:

A. Basal leaves relatively small, 0.5–2.5 cm. long, usually broadly rounded or truncate at apex; stems of rosettes bright red ..... 1a. *S. obtusatum* ssp. *typicum*

AA. Basal leaves usually larger, 1–3.0 cm. long, usually retuse at apex; stems of rosettes pale red or pink ..... 1b. *S. obtusatum* ssp. *boreale*

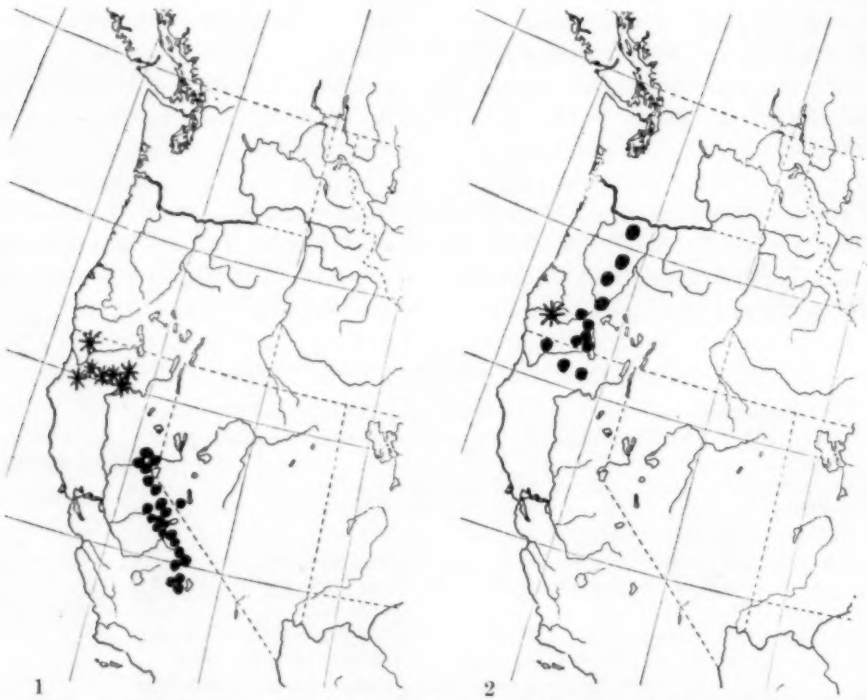

FIG. 1. Distribution of *Sedum obtusatum*, ssp. *typicum* (dots) and ssp. *boreale* (stars). FIG. 2. Distribution of *Sedum oregonense* (dots) and *S. glanduliferum* (star).

1a. SEDUM OBTUSATUM A. Gray, ssp. TYPICUM[2]

Sedum obtusatum A. Gray, Proc. Am. Acad. **7**: 342. 1868. TYPE specimens are in Gray Herbarium. Type sheet bears four collections from an equal number of localities: Vernal Falls; Yosemite Valley; Mt. Hoffman; and a peak in the Sierra Nevada. The specimen from Yosemite Valley, collected by J. Torrey, 1865, no. 143, is fragmentary and perhaps referable to *S. spathulifolium*. The other three specimens seem to be closely similar to each other and agree with Gray's original diagnosis. I have visited and collected plants at both Vernal Falls and Mt. Hoffman.

[2] Regarding the use of the epithet *typicus*, the following quotation from Gentes Herbarum (4[8]: 292. 1940) will explain my usage in this paper and elsewhere. "As employed by the writer, following Article 30, Recommendation 18 of the International Rules of Botanical Nomenclature, the epithet var. *typica* is not regarded as a new name, but as a parenthetical practical device to permit accurate designation of the typical element of a species. It has no nomenclatorial standing and does not require the citation of an authority. Whenever a variety or a subspecies is described or placed in a species, the typical element of that species automatically becomes variety or subspecies typica."

Gormania obtusata (A. Gray) Britton, Bull. N. Y. Bot. Gard. **3**: 29. 1903.

Gormania Hallii Britton, Bull. N. Y. Bot. Gard. **3**: 29. 1903. TYPE specimen, at the New York Botanical Garden, is from the vicinity of Tuolumne Meadows, in the Canadian Zone, at 8500–9500 ft. alt., Yosemite National Park, Calif., July, 1902, *H. M. Hall and E. B. Babcock 3545*. I have collected specimens on Lembert Dome, the type locality, at the eastern end of Tuolumne Meadows. These plants closely match my collections from Mt. Hoffman, and except for their later development, which is to be expected because of the higher altitude, are fair matches for plants from the region of Yosemite Valley. The shape of the sepals is not sufficiently different or reliable to distinguish this population.

Gormania Burnhami Britton, Bull. N. Y. Bot. Gard. **3**: 30. 1903. TYPE specimen, at the New York Botanical Garden, is from along the trail between Lake Eleanor and Lake Vernon, Tuolumne Co., Calif., July 16, 1894, *S. H. Burnham*. I have collected plants at the type locality. As the flowers mature, the petals fade to pink, as is the condition in plants in the Yosemite Valley. I find no basis to segregate this from the common population of the Sierra Nevada.

Cotyledon obtusata (A. Gr.) Fedde, Just's Bot. Jahresbericht **31** (1): 827. 1904.

Cotyledon Burnhamii (Britt.) Fedde, ibid.

Cotyledon yosemitensis Fedde, ibid. Based on *Gormania Hallii* Britton.

Echeveria obtusata (Gray) Nels. & Macbr., Bot. Gaz. **56**: 476. 1913.

Echeveria Brittonii Nels. & Macbr., Bot. Gaz. **56**: 476. 1913. Based on *Gormania Hallii* Britton.

Sedum rubroglaucum Praeger, Jour. Bot. **57**: 51. 1919. Described from plants sent by H. M. Hall, originally collected along the Short Trail, Yosemite Valley. I see no reason for distinguishing this from *S. obtusatum*. The crimson stem and glaucous leaves are both characteristic of the species, while the larger flower-size is not significant.

Sedum obtusatum var. *Hallii* (Britton) Smiley, Univ. Calif. Pub. Bot. **9**: 213. 1921.

Sedum Hallii (Britton) Praeger, Jour. Roy. Hort. Soc. **46**: 241. 1921.

Sedum Burhamii (Britton) Berger *in* Engl. & Prantl, Nat. Pflanzenfam. ed. 2, **18a**: 451. 1930.

Echeveria Hallii Berger, pro synon., ibid. 458.

Perennial with rootstocks to 5 mm. thick, bearing rosettes of thick, fleshy, spatulate leaves, obtuse or rounded at apex, glaucous, usually suffused with red or pink, 0.5–2.5 cm. long and 0.2–0.7 cm. wide; spreading by the production of numerous offsets, of which the stems are red; floral shoots erect, 3–16 cm. high, glabrous throughout, often suffused with red; cauline leaves alternate, oblong-spatulate, spurred, reduced upwards; inflorescence a paniculate cyme, 1.5–11 cm. long and 1.5–5 cm. broad; floral bracts spatulate to linear-oblong; sepals ovate-lanceolate, obtuse, erect, green, suffused with pink in age, 2 to 4 mm. long, united for 1 mm. at base; petals erect below and connivent for 2/5 their length, somewhat spreading above and keeled dorsally, oblong-lanceolate, 6–9 mm. long, "lemon yellow" when fresh, fading to buff or pinkish in age; stamens 4–6 mm. long, anthers yellow, filaments pale yellow;

nectar-scales transversely linear, about 0.8 mm. wide and 0.2 mm. long; carpels 6–7 mm. long, erect, greenish yellow to pinkish, becoming red in fruit.

The distribution of ssp. *typicum* is in the Sierra Nevada from Kaweah Peaks, Tulare Co., Calif., north to the headwaters of the Feather River, Plumas Co., and east to Aurora, Nevada. The altitudinal distribution is from 5000 to 13,000 ft. Habitat is usually on exposed rocks, in crevices and among boulders, occasionally in woods on rocky slopes.

Specimens seen: Highest altitude—11,000–13,000 ft., Lake of Islands, Kaweah Peaks, Tulare Co., Calif., *W. R. Dudley 2394* (DS); lowest altitude —5000 ft., Nevada Falls, Yosemite National Park, *R. T. Clausen & H. Trapido 4801* (BH, CU); northernmost—Feather River Region, Lake Center Camp, Plumas Co., Calif., *Anna Head* (CAS); easternmost—Aurora, Mineral Co., Nevada, *Mrs. J. D. Wright* (SBM); westernmost—Emigrant Gap, Placer Co., Calif., *Mrs. C. E. Miller* (CAS); southernmost—same as highest altitude; oldest—1860–62, Mt. Hoffman, *W. H. Brewer 1678* (GH). Number of collections seen—136.

The flowering time is from June to July; the fruiting time from July to August. Depending on the altitude and exposure, the leaves vary in size and in redness, also the flowers vary somewhat in size and in number in the inflorescence, but these fluctuations seem unworthy of nomenclatorial recognition. Specimens from Donner Lake, *A. A. Heller 7105* (NY, US) were given a manuscript name by J. N. Rose, but I do not regard them as sufficiently different to deserve taxonomic recognition.

A plant from Nevada Falls (*R. T. C. 4801*) and another from Lake Vernon (4810), both in Yosemite National Park, have a $2n$ number of 30. Another specimen from the slope of Mt. Hoffman (*R. T. C. 4823*) has an n number of 15. Since genetical work has not been carried on in the present investigation, there is no information regarding the compatibility of *S. obtusatum* with *S. oregonense* and the various subspecies of *S. laxum*, its nearest allies. Should these be freely interfertile, they ought all to be treated as subspecies of *S. obtusatum*. Each of these populations, here treated as species on a basis of morphological differences, occupies a distinct range.

S. obtusatum is relatively common in the horticultural trade, where it is generally correctly listed. The plant requires good drainage and much sunlight.

1b. SEDUM OBTUSATUM ssp. **boreale** Clausen, ssp. nov.—Planta foliis majoribus quam ssp. *typicum*, 1–3 cm. longis, plerumque retusis ad apicem; caules rosellarum roseatae.

Flowering plants relatively larger than ssp. *typicum*, 8–20 cm. high, rosette leaves spatulate, usually retuse at apex, 1–3 cm. long and 0.4–1.3 cm. wide, somewhat glaucous, occasionally reddish on the margins; stems of the offsets pale red or pink; floral shoots erect, glabrous, often suffused with pink; cauline leaves oblong-spatulate, spurred, reduced upwards; inflorescence an elongate paniculate cyme, 2–12 cm. long and 1.5–5.0 cm. wide; floral bracts spatulate to narrowly linear; sepals ovate, acute, 2–3 mm. long, united at base, green; petals erect below and connivent for 2/5–3/5 their length, somewhat spreading above, oblong-lanceolate, 6–7 mm. long,

pale to deep yellow, becoming white or pink with age; stamens 5–6 mm. long; carpels 6–7 mm. long. Type in the herbarium of the Department of Botany, Cornell University, from rocky slope, east side of Mud Creek Canyon, Mt. Shasta, Calif., July 26, 1940, *R. T. Clausen and H. Trapido 4952;* isotypes in the Bailey Hortorium and elsewhere.

Ssp. *boreale* occurs at altitudes from 4000–7500 ft. in the Southern Cascades and Coast Ranges of northern California.

Specimens seen: Highset altitude—6500–7500 ft., Caribou Basin, Salmon-Trinity Alps, Siskiyou Co., Calif., *J. T. Howell 13450* (CAS); lowest altitude—4000 ft., Bear Wallows, trail to Preston Peak, Del Norte Co., *Doris K. Kildale 8800* (DS); northernmost—Little Grayback, Siskiyou-Del Norte County Line, *Edward Lee* (DS); easternmost—east side of Mud Creek Canyon, Mt. Shasta, Siskiyou Co., *R. T. C. 4952* (BH, CU); westernmost—same as lowest altitude; southernmost—same as highest altitude; oldest—June 15–30, 1897, Mt. Shasta, Siskiyou Co., *H. E. Brown 440* (DS); regarding this collection, there is reason to doubt whether the plants were collected on Mt. Shasta or elsewhere. Number of collections seen—21.

The flowering time of ssp. *boreale* extends from late May to July, depending on the altitude and exposure. The seeds mature in August.

Principal variations are in the color of the flowers and in the length of the inflorescence. The petals are usually yellow when fresh, but sometimes very pale, almost white. With age, they tend to become white or pink. The inflorescence is characteristically long and narrow, with ascending slender branches, but this varies with the age of the plant and probably with the habitat.

A plant of *R. T. C. 4952*, the type collection, from Mt. Shasta, is $2n = 30$. No other collections of this subspecies have been investigated cytologically. In shape and size, the chromosomes appear similar to those of ssp. *typicum*.

2. SEDUM GLANDULIFERUM (Hend.) M. E. Peck, Man. Higher Plants Ore. 361. 1941.

Cotyledon glanduliferum L. F. Henderson, Rhodora **32**: 26. 1930. TYPE is in the herbarium of the University of Oregon, Eugene, Oregon, from along the trail 3 miles below Alameda, Rogue River, Josephine Co., Oregon, June 1, 1928, *Mr. and Mrs. J. R. Leach 1599.*

Gormania glandulifera L. F. Henderson pro synon., in Peck, ibid.

Perennial with rootstocks to 1 cm. thick, bearing compact clusters of stiff, ascending, rather flat, oblong-spatulate leaves, somewhat glaucous, glandular-crenulate, to 4 cm. long, 1 cm. wide and 2 mm. thick, with apex subacute and grooved; floral stems erect or abruptly decumbent at base, to 3 dm. high, glabrous below, densely glandular above; cauline leaves alternate, oblong-spatulate, sessile, 1.1–2.8 cm. long and 0.5–1.2 cm. wide, glandular-hairy; flowers in a densely glandular two-three parted cyme; floral shoot recurved before anthesis; floral bracts oblong-spatulate, glandular-ciliate, 0.5–1.4 cm. long below, much reduced upwards; pedicels 2 mm. long; sepals erect, ovate or lanceolate, obtuse or acute, united for 1–2 mm. at base, 5–6 mm. long, densely glandular; petals erect, primrose-yellow to greenish yellow, oblong-lanceolate, abruptly acuminate-attentuate, densely glandular,

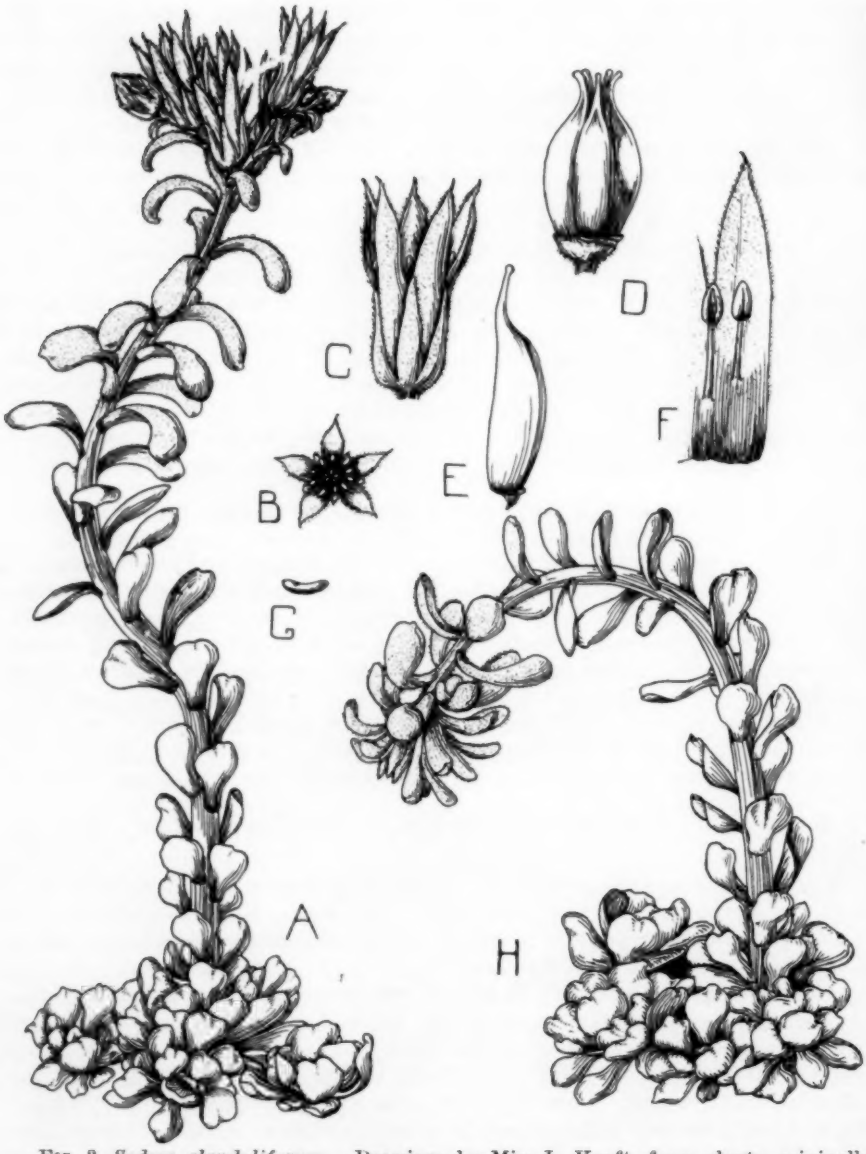

FIG. 3. *Sedum glanduliferum*. Drawings by Miss L. Kraft, from plants, originally from type locality, grown at Ithaca, N. Y. A. Habit sketch ($\times \frac{1}{2}$). B. Flower from above ($\times 1\frac{3}{5}$). C. Flower from side ($\times 1\frac{3}{5}$). D. Carpels ($\times 2\frac{2}{5}$). E. Single carpel ($\times 3\frac{1}{2}$). F. Petal and two stamens ($\times 2\frac{3}{5}$). G. Nectar scale ($\times 4$). H. Habit sketch of plant before flowering ($\times \frac{1}{2}$).

14 mm. long, with the margins connivent for ¼ their length; stamens 4–7 mm. long, with anthers oblong, 0.8–1 mm. long, rounded apically and truncate basally, deep yellow; fresh nectar-scales normally transversely linear; carpels erect, 6–10 mm. long, with short stout styles to 2 mm. long; seeds oblong-pyriform, yellow-brown, finely-striate.—In the original description Henderson commented particularly on the red color of the plant, but I have not been impressed by this character. A plant cultivated in the Santa Barbara Botanic Garden, originally collected by Reid Moran at the type locality, was dark green, only somewhat glaucous. Plants at the type locality, observed by me on July 31, 1940, had the leaves glaucous, somewhat suffused with red or purple, but not decidedly so.

S. glanduliferum is known only from the type locality along the Rogue River below Alameda, Oregon, in the Pacific Border Province (fig. 2).

Specimens seen: Two herbarium collections, three cultures of living plants grown at Ithaca, New York, and one at Santa Barbara, Calif., all from type locality.

Flowering time is June.

Representatives of two collections from the type locality, *Moran 403* and *R. T. C. 5014*, investigated cytologically, are $2n = 30$.

Illustration: Figure 3.

3. SEDUM OREGONENSE (Watson) M. E. Peck, Man. Higher Plants Ore. 361. 1941.

Cotyledon oregonensis S. Wats., Proc. Am. Acad. **17**: 373. 1882. The TYPE, in the Gray Herbarium, is the collection of J. and T. J. Howell, no. 322, July 1880, from the Cascade Mts., Oregon. Watson mentioned northern Oregon as the nativity of the species and described the petals as pale yellow. Mt. Hood probably is the original locality. Plants collected by me near Crater Lake closely match the type.

Gormania watsoni Britton, Bull. N. Y. Bot. Gard. **3**: 29. 1903.

Echeveria Watsonii (Britton) Nels. & Macbr., Bot. Gaz. **56**: 476. 1913.

Sedum Watsoni (Britton) Tidestrom, Proc. Biol. Soc. Wash. **40**: 119. 1927.

Perennial with well-developed, much branched, spreading rootstocks to 7 mm. thick, bearing rosettes of fleshy, spatulate leaves, rounded, truncate or slightly retuse at apex, glaucous, yellow-green, often suffused with pink or red, 1–2.8 cm. long, and 0.4–1.1 cm. wide; spreading by the frequent production of offsets of which the stems are green suffused with pink; floral shoots erect, 6–27 cm. high, glabrous, pinkish to red; cauline leaves alternate, oblong-spatulate to almost orbicular, spurred, 0.5–1.2 cm. long; inflorescence paniculate, 1.5–9 cm. long and 1.5–7 cm. wide, usually widest and densest above; floral bracts spatulate, orbicular or linear; sepals ovate, acute, erect, 2–3 mm. long, united for 1 mm. at base; petals oblong, blunt, erect below and connivent for ⅙ to ⅔ their length, somewhat spreading above, 7 to 8 mm. long, white to creamy white; stamens 4–6 mm. long, anthers salmon-pink; nectar scales transversely linear, about 0.8 mm. wide and 0.2 mm. long; carpels 6–7 mm. long, erect.

S. oregonense occurs in the Cascade Mountains of Oregon and northern California, at elevations from 5500 to 7800 ft. (fig. 2). The habitat usually is exposed rocky slopes, cliffs or steep mountain-sides.

Specimens seen: Highest altitude—7800 ± ft., Mt. Jefferson, Ore., *M. E. Peck 9163* (BH); lowest altitude—5200 ft., Mt. Jefferson, Ore., *M. W. Gorman 2831* (DS); northernmost—Bluegrass Ridge, Mt. Hood, Ore., *J. W. Thompson 3323* (DS) (Specimens from bluffs of the ocean, Ilwaco, Pacific Co., Wash., July 26, 1886, *L. F. Henderson 330* (DS) are doubtfully to be referred here. Further material is needed from that locality); easternmost—same as northernmost; westernmost—Preston Peak, Siskiyou Co., Calif., *Doris K. Kildale 8585* (BH, DS); southernmost—Mt. Eddy, Siskiyou Co., Calif., *L. E. Smith 433* (CAS); oldest—1880, Cascade Mts., Ore., *J. & T. J. Howell 322* (GH, NY, DS). Number of collections seen—50.

Flowering time is July; fruiting time, August.

Throughout its range, *S. oregonense* seems constant in its characters. In the horticultural trade, a variety *rosea* is offered.

Two populations from the region of Crater Lake have been investigated cytologically. These both have a $2n$ number of about 90. All other species of the section *Gormania*, which have been studied cytologically, with the exception of one cultivated plant of unknown source and which possibly is this species, have a $2n$ number of 30. Presumably, *S. oregonense* does not interbreed with its relatives, both because of geographic and genetic barriers. No experimental crossing has been attempted. *S. oregonense* is nearest to *S. obtusatum*. The relationships of these two species still require further field study, particularly at places like Mt. Eddy where both occur.

S. oregonense is rather frequent among fanciers as a rock-garden subject. In the trade, it is usually listed as *Gormania watsonii*.

4. Sedum laxum (Britton) Berger.

This is a glabrous perennial with broadly to narrowly spatulate retuse rosette-leaves, pink or pinkish-white flowers and lanceolate, acute or acuminate sepals. The collective species ranges from north-central California to southwestern Oregon and is composed of five subspecies. These are separated in the following key:

A. Plants tall and robust, 25–40 cm. high; leaves dark green, not glaucous; petals deep pink ..... 4b. *S. laxum* ssp. *typicum*

AA. Plants not as tall as above, 10–25 cm. high; leaves yellow-green or blue-green, usually glaucous; petals pink, pale pink to white suffused with pink ..... B

B. Inflorescence congested; rosettes closely crowded, forming a dense mat, with the leaves rather thin ..... 4d. *S. laxum* ssp. *retusum*

BB. Inflorescence lax; rosettes not closely crowded, forming a loose mat, with the leaves thick and leathery C

C. Rosette-leaves very broad, 2.0–3.0 cm. wide, triangular, obcordate, sometimes not glaucous; petals pale pink to white. 4c. *S. laxum* ssp. *latifolium*

CC. Rosette-leaves narrow, 0.3–2.0 cm. wide, oblong-oblanceolate or spatulate, usually glaucous; petals pink ..... D

D. Cauline leaves oblong-spatulate, longer than broad. 4a. *S. laxum* ssp. *perplexum*

DD. Cauline leaves cordate to subcordate, about as broad as long ..... 4e. *S. laxum* ssp. *heckneri*

4a. Sedum laxum ssp. **perplexum** Clausen, ssp. nov.—Planta parva, 7–

15 cm. alta; folia rosellarum oblonga-oblanceolata vel spatulata, glauca, 0.5–2.5 cm. longa, 0.3–1.4 cm. lata; folia caulina oblonga-spatulata, longiores quam lata; petala roseata.

Flowering plants relatively small, 7–15 cm. high; rosette-leaves oblong-oblanceolate or spatulate, glaucous, rounded, truncate or somewhat retuse at apex, 0.5–2.5 cm. long and 0.3–1.4 cm. wide; rosettes forming loose mats, but not densely crowded; cauline leaves oblong-spatulate, longer than broad; inflorescence a paniculate cyme, broader than long, 2–6 cm. wide and 2–4 cm. long; sepals lanceolate, acute, 4–5 mm. long; petals pink, 8 to 10 mm. long. TYPE in the Bailey Hortorium, from cliff near mouth of Rogue River, Oregon, July 8, 1919, *M. E. Peck 8703.*

Ssp. *perplexum* occurs at low altitudes in the Pacific Border Province from Del Norte Co., California, to Curry Co., Oregon, and inland to Jackson Co., Oregon.

Specimens seen: Highest altitude—6500 ft., Salmon Summit via Horn Creek Trail, Siskiyou Co., Calif., *Doris K. Kildale 5362* (DS); lowest altitude—near sea-level, type collection, *M. E. Peck 8703* (BH, WILLU); northernmost and westernmost—type collection; easternmost—Steen's Butte, Jackson Co., Ore., *M. E. Peck 19429* (WILLU); southernmost—Gordon Mt., Del Norte Co., Calif., *Doris K. Kildale 9930* (BH); oldest—Sept. 11, 1912, trail from Waldo to Black Butte, Siskiyou Co., Calif., *Alice Eastwood 2142* (CAS). Number of collections seen—17. A collection from Trinity Co., Calif., July, 1880 (CAS 136352), would be both the oldest and southernmost record, but the specimens are not sufficiently complete for certain identification.

Flowering time is from June through July. The fruiting shoots and capsules may persist through the winter.

This subspecies passes imperceptibly into the other variants. Specimens intermediate between it and ssp. *typicum* are illustrated by my collection *no. 5015* from a steep slope on the north side of the Rogue River 6 miles above Galice, Josephine Co., Ore. In stature, shape and nature of rosette-leaves and type of inflorescence, this collection stands between the two, but the flowers are white on opening and then become pale pink, in this respect resembling ssp. *latifolium.* Ssp. *perplexum* also shows certain tendencies towards *Sedum oregonense* on the one side and towards ssp. *heckneri* on the other. It may possibly be only a phase of the latter.

Chromosomal data are available for only one collection of ssp. *perplexum.* This is a cultivated specimen of unknown origin. In this, $2n = 30$. A plant of my collection *no. 5015* and a similar intermediate plant from the same region both are $2n = 30$.

From the horticultural trade, ssp. *perplexum* has been received as *Gormania laxa.* It is a desirable subject for the rockery.

4b. SEDUM LAXUM (Britton) Berger, ssp. TYPICUM.

Gormania laxa Britton, Bull. N. Y. Bot. Gard. **3**: 29. 1903. The TYPE, at the New York Botanical Garden, is the collection of Thomas Howell, June 4, 1884, from Waldo, Oregon.

Cotyledon Brittoniana Fedde, Just's Bot. Jahresbericht **31** (1): 827. 1904. Based on *Gormania laxa* Britton.

Echeveria Gormanii Nels. & Macbr., Bot. Gaz. **56**: 476. 1913.

Sedum laxum (Britton) Berger, Engl. & Prantl, Nat. Pflanzenfam. ed. 2, **18a**: 451. 1930.

Stout, with rootstock to 1.5 cm. thick, bearing rosettes of stiff, flat, narrowly spatulate leaves, truncate or retuse at apex, dark green, to 4.5 cm. long and 1.7 cm. wide; floral stems stout, to 1.0 cm. thick, erect throughout development, to 40 cm. high, glabrous; cauline leaves alternate, oblong-spatulate; inflorescence 5–17 cm. long and 10.5 cm. across; floral bracts spatulate to linear; sepals ovate-lanceolate, with their margins connivent below for one-third their length, spreading above, 8 to 10 mm. long; stamens 5 to 6 mm. long; nectar scales transversely linear; carpels erect, with styles somewhat divergent, to 8 mm. long; seeds pyriform, yellow-brown, 1.2–1.5 mm. long.

The typical phase of *Sedum laxum* is known from only two localities, both in Josephine Co., Ore., the region of the type locality, at an elevation of 2000 ft. in the Rogue River Basin, at Waldo, and in yellow pine woods on the east slope of Eight Dollar Mountain, *Elmer Applegate* (DS). I collected and observed the species at Waldo on August 1, 1940 (*R. T. C. 5018*), also I have examined five other collections from that locality. The plant is abundant there on dry rocky slopes. The rosettes are glaucous, green to purple or red, with the leaves finely crenulate and minutely spotted with white. This has the appearance of a distinct species with its large rosette and spatulate cauline leaves, but intermediates occur between the large plants, as they grow at Waldo, and ssp. *perplexum*. Applegate's collection (DS 247453) from near Pilot Rock, Siskiyou Mts., Jackson Co., Ore., illustrates this intergradation.

Two authentic specimens from the type locality, investigated cytologically, are $2n = 30$.

Typical Sedum laxum seems not to be in the trade, although, because of its large size, it is more showy than any of the other subspecies. I have seen one cultivated specimen from a garden in San Francisco. At Waldo, the flowering time is the middle of June.

4c. SEDUM LAXUM ssp. **latifolium** Clausen, ssp. nov.—Planta 15–30 cm. alta; folia rosellarum triangulato-obcordata vel late spatulata, latissima, non glauca vel paulum glauca, 1.5–4 cm. longa, 0.7–3 cm. lata; folia caulina spatulata, longiores quam lata; petala roseata vel alba.

Flowering plants 15–30 cm. high; rosette-leaves very thick, triangular-cordate or broadly spatulate, very broad, deeply emarginate at apex, either yellow-green and not glaucous or somewhat glaucous, 1.5–4 cm. long and 0.7–3 cm. wide; cauline leaves spatulate, longer than wide; inflorescence a paniculate cyme, longer than broad, 2.5–8 cm. long and 1–4 cm. wide; sepals lanceolate, acute, 3–4 mm. long; petals 7–10 mm. long, oblong-lanceolate, pink or white suffused with pale pink. TYPE in the Bailey Hortorium, from rocky slope along Smith River 24 miles northeast of Crescent City, Del Norte Co., Calif., July 24, 1940, *R. T. Clausen 4941*.

Ssp. *latifolium* is at present known only from the general region of the type locality, where it occurs on steep slopes and rocky bluffs at an elevation of about 1500 feet. Besides the collection cited as type, at least seven other collections have been made. The localities for these are Smith River Canyon, Smith River near Adams Station, near Gasquet, Gasquet Mountain, Gasquet

to Patricks and Patrick Creek. Flowering time is late June and early July.

A plant of my collection *4941*, grown in a greenhouse at Ithaca, New York, is $2n = 30$. A plant of a collection by Moran (*no. 406*) from the entrance to the Siskiyou National Forest, 2 miles above Hiouchi Grove on the main highway up the Smith River from Crescent City, Calif., to Grants Pass, Ore., also is $2n = circa\ 30$.

4d. SEDUM LAXUM ssp. **retusum** (Rose) Clausen, comb. nov.

Gormania retusa Rose. Bull. N. Y. Bot. Gard. **3**: 31. 1903. The TYPE specimen, in the United States National Herbarium, is the collection of A. A. Heller, Aug. 6, 1902, from Sanhedrin Mountain, 5000 ft., Lake Co., Calif.

Gormania Eastwoodiae Britton, Bull. N. Y. Bot. Gard. **3**: 31. 1903. I have seen the TYPE in the herbarium of the California Academy of Sciences and an isotype at the New York Botanical Garden. The type locality is Red Mt., Mendocino Co., Calif.

Cotyledon retusa (Rose) Fedde, Just's Bot. Jahresbericht **31** (1): 827. 1904.

Cotyledon mendocinoana Fedde, ibid. Based on *Gormania Eastwoodiae* Britton.

Sedum sanhedrinum Berger, Engl. & Prantl, Nat. Pflanzenfam., ed. 2, **18a**: 451. 1930.

Sedum Eastwoodiae Berger, loc. cit.

Rootstocks rather stout, bearing many rosettes closely crowded and forming a dense mat; leaves obovate to spatulate, retuse or obtuse, blue-green, glaucous, 2.5 cm. long, or less, thinner than in the other subspecies; floral stems 10–15 cm. tall; inflorescence congested, about 6 cm. long; sepals ovate, acute, 3 mm. long; corolla pink or red, 6–7 mm. long, with the petals connivent for one-fourth to one-third their length.

Range of ssp. *retusum* is in Lake and Mendocino Counties in the Pacific Border Province of northern California. Besides the type and other collections from the original locality, I have seen specimens from Buck Rock Ridge, Mendocino Co., Calif., *Mrs. E. O. Murphey* (CAS).

A plant from Mendocino Co., Calif., no. 28. 3 in University of California gardens, sent by Professor T. H. Goodspeed and cultivated at Ithaca, New York, has a $2n$ number of 30. In the small rosette-leaves and flowers, this seems near to *S. obtusatum*, but in that species the corolla is yellow and the inflorescence is not so dense, also the leaves are not retuse.

Specimens from Klamath, Humboldt Co., Calif. (DS 9854), are intermediate between ssp. *retusum* and *perplexum*, and in their taller stems, tend towards ssp. *typicum*.

4e. SEDUM LAXUM ssp. **heckneri** (Peck) Clausen, comb. nov.

Sedum Heckneri M. E. Peck, Proc. Biol. Soc. Wash. **50**: 121. 1937. TYPE seen in the herbarium of Willamette University, Salem, Oregon. This was collected on a dry cliff along the Middle Fork of the Applegate River four miles above the mouth of Carberry Creek, Jackson County, Oregon, June 26, 1931, *M. E. Peck, no. 16421.*

Plant glaucous; rootstocks stout, freely branched; leaves of the rosettes minutely crenulate, spatulate or obovate—spatulate, truncate to emarginate

at apex, 1–2.5 cm. long; flowering stems 1–2 dm. high, stout, very leafy, with the leaves orbicular to broadly oblong, 0.5–2 cm. long, strongly cordate clasping, spreading at base and curved upward; inflorescence a somewhat globose cluster, 2–4 cm. long and 3–5 cm. wide; calyx 2–4 mm. long, parted nearly to the base, with the lobes ovate, acute or subacute; petals pink, erect, 8–10 mm. long, oblong-lanceolate, obtuse or acute, connivent ¼ their length or sometimes quite free to base; stamens 6–8 mm. long; carpels 8 mm. long; styles divergent.

The distribution is in the Pacific Border Province, in northwestern California and southwestern Oregon, where it occurs on dry cliffs, rocky talus and rocky crests.

Specimens seen: Highest altitude—4590 ft., Horse Mountain, Humboldt Co., Calif., *Doris K. Kildale 2167* (DS); lowest altitude—near sea-level, Rogue River at Gold Beach, Curry Co., Ore., *Doris K. Kildale 6162* in part (DS); northernmost and westernmost—*Kildale 6162;* easternmost—4 miles east of Fork of Salmon, Siskiyou Co., Calif., *Alice Eastwood and J. T. Howell 5056* (CAS); southernmost—*Kildale 2167;* oldest—June 9, 1926, *Kildale 2167*. Number of collections seen—7.

Flowering time is June to July. No information is available regarding the cytology and breeding relationships of this subspecies. It is nearest to ssp. *perplexum*, from which it differs primarily in the shape of the cauline leaves. From ssp. *typicum* it differs in the cauline leaves as well as in the size and form of the inflorescence.

SUMMARY

Gormania is redefined as a subgenus of *Sedum* comprising three sections: *Eugormania, Rosulata* and *Oreganica*. The last is described as a new section. *Eugormania* includes four species. Nomenclatorial innovations are *Sedum obtusatum* ssp. *boreale, S. laxum* ssp. *perplexum, S. l.* ssp. *latifolium, S. l.* ssp. *retusum* and *S. l.* ssp. *heckneri*.

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NOTE:—Since the above was written, Mr. Reid V. Moran has brought to my attention the binomial *Sedum glanduliferum* Gussone, published in 1827. This name is an earlier homonym of *S. glanduliferum* (Henderson) M. E. Peck. Accordingly I take pleasure in renaming as *Sedum moranii* Clausen nom. nov. the species based on *Cotyledon glandulifera* L. F. Henderson, Rhodora **32**: 26. 1930.

BULLETIN OF THE TORREY BOTANICAL CLUB
69(1): 41–43 JANUARY, 1942

CHROMOSOME STUDIES IN SEDUM, SUBGENUS GORMANIA, SECTION EUGORMANIA

LILLIAN HOLLINGSHEAD

The chromosomes described in this report were studied for Dr. R. T. Clausen to help him in classifying the plants in question, and his conclusions are reported in a paper in this issue of the BULLETIN (Clausen 1942).

Root tips were fixed in chrom-acetic-formalin and imbedded according to Randolph (1935). Sections were cut 8 μ in thickness and stained with crystal violet. The drawings were made with the help of a camera lucida and are reproduced at a magnification of approximately 3500 diameters.

The species and subspecies represented, and the number of plants examined are given in table 1. Chromosome numbers in *S. spathulifolium* are included for comparison, though it belongs to another section of the subgenus (Clausen 1942).

TABLE 1

Chromosome numbers in Sedum, subgenus Gormania

Species	Subspecies	Number of plants	Chromosome number	
			2n	n
S. obtusatum	*typicum*	2	30	
S. obtusatum	*typicum*	1		15
S. obtusatum	*boreale*	1	30	
S. glanduliferum		2	30	
S. oregonense		3	90 ±	
S. laxum	*perplexum*	1	30	
S. laxum	*typicum*	2	30	
*S. laxum**		1	30	
*S. laxum**		1	30	
S. laxum	*latifolium*	2	30	
S. laxum	*retusum*	1	30	
S. spathulifolium		3	30	

* Intermediates between *perplexum* and *typicum*.

The diploid number is 30 throughout excepting *S. oregonense* in which the three plants examined have about 90 chromosomes. These plants are, therefore, hexaploid in relation to the other species.

The chromosomes in all species are very small, and in late prophase and at metaphase appear roughly circular or elliptical in cross section (figs. 1–5). There is no consistent visible evidence of the two-armed structure, typical of mitotic chromosomes in general, and which has been found char-

acteristic of *Sedum*, even in those species which have the smallest chromosomes (Baldwin 1935, 1936, 1937, 1939, 1940). Moreover one plant of *S. debile* which Britton included in *Gormania* (Clausen 1942) has much larger markedly two-armed chromosomes quite different from those of *Gormania*. Dr. Clausen includes it with *S. divergens* which preliminary studies show has about 16 diploid two-armed chromosomes.

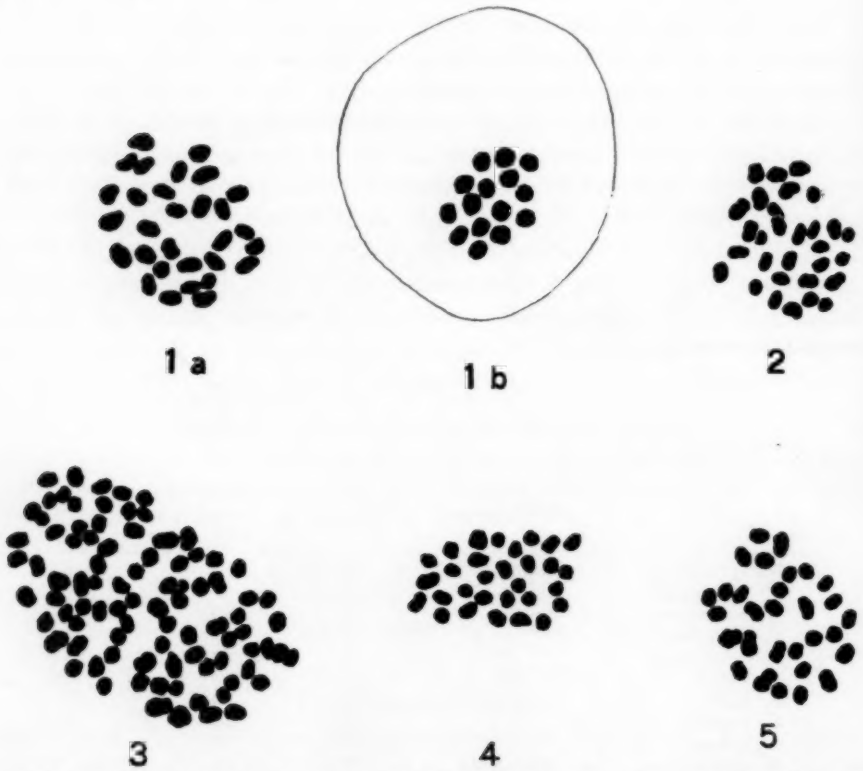

FIG. 1. *S. obtusatum typicum*. (a). Mitotic metaphase ($2n = 30$). (b). Meiotic metaphase ($n = 15$). FIG. 2. *S. glanduliferum* ($2n = 30$). FIG. 3. *S. oregonense* ($2n = 90 \pm$). FIG. 4. *S. laxum typicum* ($2n = 30$). FIG. 5. *S. spathulifolium* ($2n = 30$).

As metaphase proceeds, each chromosome divides into two daughter chromosomes roughly spherical in shape and they move apart to the poles, in appearance very much like tiny meiotic chromosomes. The constricted appearance of some chromosomes in the figures represents in each case the polar view of a dividing chromosome in which one daughter lies slightly to one side of the other.

The outlines are not so clear as the black and white figures indicate, but in each plant recorded metaphases were found in which the chromosomes

were well separated and readily countable, except in the case of those with 90 odd chromosomes which are not quite so clear.

There are apparent size differences among the chromosomes in one plant, which may be due in part to differences in orientation. No particular chromosomes could be identified. Neither could the complexes of the 30-chromosome species be distinguished from one another. Metaphases can be found in which the chromosomes appear to be larger than others of the same species. This can arise from the fact that early metaphase chromosomes appear larger than they do at late metaphase. As metaphase proceeds and each chromosome prepares to divide, it becomes oriented with the axis of division strictly toward the poles and the upper small daughter chromosome wholly obscures the one below, whereas earlier the orientation may be such as to show parts of both daughter chromosomes.

The one plant (*S. obtusatum*) examined at meiosis had the expected 15 pairs of chromosomes (fig. 1 b).

Baldwin (1939), who has made numerous studies in Crassulaceae, has found this family very diverse karyologically, but nevertheless within restricted groups, chromosome size is fairly uniform. The study here reported supports his conclusions, for the chromosomes throughout the group have a characteristic form and size. It further illustrates the value of a cytotaxonomic approach to an understanding of the family.

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BULLETIN OF THE TORREY BOTANICAL CLUB
69(1): 44–64 JANUARY, 1942

NEW AND UNUSUAL CORTINARII FROM MICHIGAN, WITH A KEY TO THE NORTH AMERICAN SPECIES OF SUBGENUS BULBOPODIUM[1]

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During the last part of August and the first week in September of 1940, southeastern Michigan received an exceptionally heavy rainfall. As a result, agarics fruited prolifically during September even though the weather during the remainder of the month was no wetter than usual. The most conspicuous element in the agaric flora was the numerous species of the genus *Cortinarius*. On no previous occasion, either in the Olympic Mountains of Washington or along the northern coast of California where I (7) had found *Cortinarii* most abundantly, have I seen so many species or such large quantities of material as appeared around Ann Arbor early in the fall of 1940. There were relatively few members of the subgenera *Myxacium*, *Inoloma*, and *Dermocybe*, but this lack was more than offset by *Bulbopodium*, *Phlegmacium*, *Telamonia*, and *Hydrocybe*. Nearly all the *Cortinarii* fruited within the space of two weeks, so that it was possible to study only a limited number. In the following account particular emphasis has been given to *Bulbopodium*, a subgenus to which I have paid special attention for the past seven years. In the other subgenera only those species with some outstanding macroscopic character have been included. By limiting myself to such species, the descriptions of the earlier mycologists, who did not study microscopic characters, can be used to some advantage.

DISCUSSION OF AND KEY TO THE NORTH AMERICAN SPECIES OF BULBOPODIUM

Since particular attention was paid to the species of *Bulbopodium*, I have given, in the following account, a list of all the members of that subgenus which I collected during the fall of 1940, a list of the additional species which at one time or another I have seen in the fresh condition, and also a list of those recognized from North America by Kauffman (3), but of which I have not seen fresh material. As a summary, a revised key to the known North American species is included. Because of lack of space, descriptions are given only for the new species or in cases of revised concepts. Descriptive accounts of the others are to be found in Kauffman (3) and in Smith (7). Murrill's (6) new species of *Cortinarius* are not included. Of those apparently belonging to *Bulbopodium*, *C. subfulmineus* keys out to *C. fulgens* and may possibly be that species. *C. subglaucopus* is undeterminable because he has not given the color of the young gills.

[1] Papers from the University of Michigan Herbarium.

The following is the list of species collected in the vicinity of Ann Arbor during the fall of 1940: *C. aggregatus, C. albidus, C. amnicola, C. arenicola, C. Atkinsonianus, C. Bouderi, C. caesiocyaneus, C. calyptrodermus, C. citrinipedes, C. corrugatus, C. elegantioides, C. fulmineus* var. *sulphureus, C. michiganensis, C. purpureophyllus, C. olivaceostramineus, C. squalidus, C. subsolitarius,* and *C. virentophyllus.*

In addition to the eighteen listed above, I have previously seen material of *C. arquatus, C. calochrous, C. calyptratus, C. cedretorum, C. glaucopus, C. herpeticus, C. intrusus, C. metarius, C. montanus, C. multiformis, C. occidentalis, C. olympianus, C. orichalceus, C. Parksianus, C. prasinus, C. purpurascens, C. scaurus, C. subpurpurascens, C. subpurpureophyllus, C. velicopia, C. volvatus.*

Of those included by Kauffman (3) in his monograph, I have not seen fresh specimens of *C. caerulescens, C. sphaerosperma, C. lilacinopes, C. glaucopoides, C. citrinellus, C. fulgens, C. elegantior, C. rubens,* and *C. sublateritius. C. fulgens* and *C. elegantior* are included in this last group simply because my collections have not checked well with existing descriptions, and I have no clear species-concepts of them based upon fresh material.

Of the thirty-four *Bulbopodia* recognized for North America by Kauffman, I have seen twenty-five in the fresh condition. Fourteen additional species have been added bringing the total number recognized for the continent up to forty-eight. In the descriptive text, all color terms within quotation marks are taken from Ridgway, *Color Standards and Color Nomenclature,* Washington, D. C., 1912. Collections cited by number have been desposited in the University of Michigan Herbarium.

Revised Key to the North American Species of Bulbopodium

1. Lamellae (and at least the apex of the stipe) at first violet purplish, blue or shades of these colors. (*C. Atkinsonianus* and *C. cedretorum* with yellowish gills are included here, as is *C. arenicola* with pallid gills) ..... 2.
1. Lamellae at first green, olivaceous, smoky or assuming shades of these colors (context and young lamellae may be slightly violaceous or blue at first in *C. montanus, C. scaurus* and *C. herpeticus*) ..... 30.
1. Lamellae yellow, fulvous, cinnamon reddish or dull rusty brown when young ..... 35.
1. Lamellae white or pallid at first ..... 42.

Lamellae at first violaceous, lilac or purplish

2. Lamellae turning purplish when bruised ..... 3.
2. Lamellae not turning purplish when bruised ..... 6.
3. Stipe stuffed to hollow; context not turning purplish; pileus yellow-ochraceous tawny ..... *C. subpurpurascens.*
3. Stipe solid, context turning purplish when bruised ..... 4.
4. Spores spheroid, 7–8 × 6–7.5 μ; pileus violet-purple ..... *C. sphaerosperma.*
4. Spores ellipsoid ..... 5.
5. Pileus blue when young, fading to gray in age ..... *C. occidentalis.*

5. Pileus umber-purplish, soon streaked with clay-color or dark reddish brown. *C. purpurascens.*
6. Spores averaging more than 10 μ long ..... 7.
6. Spores not more than 10 μ or rarely 11 μ long ..... 20.
7. Surface of pileus conspicuously corrugated ..... *C. corrugatus.*
7. Surface of pileus smooth or slightly uneven ..... 8.
8. Pileus chiefly violet or purplish ..... 9.
8. Pileus if violet or purplish quickly changing to some other color ..... 12.
9. Universal veil ochraceous buff, stipe and pileus lutescent ..... *C. velicopia.*
9. Universal veil if present white; pileus and stipe violaceous, hardly changing ..... 10.
10. Young gills faintly tinged pinkish, pileus and stipe pinkish lilac overall ..... *C. arenicola.*
10. Young gills dark or pallid violet ..... 11.
11. Gills pallid to pale violet, pileus glabrous or slightly fibrillose ..... *C. caesiocyaneus.*
11. Gills dark violet, pileus decorated with white felt-like masses of universal veil tissue. *C. calyptrodermus.*
12. Pileus normally 4–6 (7) cm. broad ..... 13.
12. Pileus normally 6–12 cm. broad ..... 17.
13. Lamellae broad, violet amethyst; pileus soon yellow, bulb white, spores 12–14 × 6–7 μ. *C. caerulescens.*
13. Not as above ..... 14.
14. Stipe 8–15 cm. long, 10–15 mm. thick, pileus dark reddish brown. *C. subpurpureophyllus.*
14. Stipe shorter, pileus yellow ..... 15.
15. Universal veil brilliant orange, stipe pinkish lilac above, bright yellow below both inside and out ..... *C. amnicola.*
15. Universal veil at most merely pale yellowish ..... 16.
16. Spores 9–12 (13) × 5–6 μ ..... *C. metarius.*
16. Spores 11–14 (15) × 6–8 μ ..... *C. arquatus.*
17. Spores averaging more than 12 μ long, surface of pileus yellow ..... 18.
17. Spores 10–12 (13) μ long, pileus variously colored ..... 19.
18. Context pale incarnate, stipe white downwards, without evident universal veil. *C. lilacinopes.*
18. Context deep violet, pileus and universal veil bright olive yellow. ..... *C. Atkinsonianus.*
19. Pileus dull purplish umber when young ..... *C. Parksianus.*
19. Pileus tawny-reddish when young, gills bright lavender ..... *C. purpureophyllus.*
19. Pileus olive-buff when young, somewhat testaceous in age, gills rather dark grayish lavender ..... *C. Boudieri.*
19. Pileus bright yellow, becoming dark red at maturity, lamellae yellow at first. *C. cedretorum.*
20. Pileus 3–7 cm. broad (occasionally larger) ..... 21.
20. Pileus 6–12 cm. or more broad ..... 27.
21. Pileus covered by a white felt-like mass of universal veil tissue at least over the disc, flesh pallid brownish, surface violet ..... *C. calyptratus.*
21. Pileus glabrous or fibrillose streaked, if with universal veil remnants the latter not becoming white ..... 22.
22. Disc of pileus bright yellow or streaked with greenish yellow due to greenish yellow veil remnants ..... 23.
22. Pileus differently colored, usually violet to whitish ..... 24.
23. Pileus glabrous, bright yellow ..... *C. calochrous.*
23. Pileus olivaceous yellow to sordid yellow over the disc, dark purplish brown toward the margin ..... *C. citrinipedes.*
24. Usually densely gregarious or cespitose ..... 26.
24. Usually solitary or scattered, occasionally 2 or 3 in a cluster ..... 25.
25. Universal veil greenish yellow ..... *C. citrinipedes.*

25. Universal veil lacking, cortina dark violet, pileus gills and stipe dark violet and hardly fading ..... *C. subsolitarius.*
25. Universal veil copious and white, pileus becoming whitish ..... *C. volvatus.*
25. Gills pinkish lilac, universal veil inconspicuous ..... *C. olympianus.*
26. Gills pinkish lilac, retaining a lilac tinge ..... *C. olympianus.*
26. Gills violet-purple at first, soon pale purplish gray ..... *C. aggregatus.*
27. Bulb large and prominently depressed, plant pale violaceous ..... *C. michiganensis.*
27. Bulb relatively small, lamellae rather broad ..... 28.
28. Context, pileus and stipe at first violet-purple, pileus at length smoky olive-gray. *C. aggregatus.*
28. Context whitish, at length lutescent ..... 29.
29. Pileus pale-orange-yellow, not streaked ..... *C. glaucopoides.*
29. Pileus slate gray, fulvous-streaked, often greenish when young or greenish gray. *C. glaucopus.*

Lamellae at first green or olivaceous or soon becoming so

30. Context and young lamellae at the very first tinged with violet, blue or purplish but lamellae very soon olivaceous ..... 31.
30. Context and gills not as above ..... 33.
31. Spores 9–11 (12) × 5.5–6.5 μ, pileus variegated with brown, tawny and slight olivaceous hues ..... *C. montanus.*
31. Spores 8–9.5 × 5–6 μ; pileus Dresden-brown to tawny ..... 32.
32. Bulb yellow from universal veil; stipe 6–10 mm. thick, lamellae narrow ..... *C. scaurus.*
32. Bulb white or whitish; stipe 10–20 mm. thick, lamellae broader than the preceding. *C. herpeticus.*
33. Stipe bluish, pileus and gills green ..... *C. virentophyllus.*
33. Stipe not bluish ..... 34.
34. Disc of cap spotted dark vinaceous red or becoming reddish over all ..... *C. orichalceus.*
34. Pileus remaining dark olive-color in age or when dried ..... *C. prasinus.*

Lamellae at first yellow, fulvous, cinnamon reddish or dull brown
(But see *C. Atkinsonianus* & *C. cedretorum* under 2 in this key.)

35. Growing in greenhouses ..... *C. intrusus.*
35. Growing in the woods ..... 36.
36. Spores not more than 10 μ long ..... 37.
36. Spores averaging more than 10 μ long ..... 38.
37. Spores ellipsoid, pileus and stipe sulphur yellow; arising from a yellow mycelium. *C. fulmineus* var. *sulphureus.*
37. Spores subglobose, 8–9 × 6–8 μ, pileus at first buff-citrine, then clay-colored. *C. citrinellus.*
37. Spores ellipsoid, gills dull brown, pileus dark brown in age ..... *C. squallidus.*
38. Taste of context decidedly bitter; pileus and universal veil yellow; spores 15–18 (20) × 7–9 μ ..... *C. elegantoides.*
38. Taste not bitter ..... 39.
39. Pileus corrugated, tawny to yellowish ..... *C. corrugatus.*
39. Pileus not corrugated ..... 40.
40. Spores more than 12 μ long ..... 41.
40. Spores 9–12 μ; pileus bright orange (*C. cedretorum* may key out here also, cap yellow, flesh lilac) ..... *C. fulgens.*
41. Pileus yellow, spores 12–15 μ long ..... *C. elegantior.*
41. Pileus dull red to orange-tawny; spores 15–18 × 7–8.5 μ ..... *C. rubens.*

Lamellae pallid at first

42. Pileus pale olivaceo-stramineus, stipe soft, becoming hollow ..... *C. olivaceostramineus.*

42. Pileus without olive tints ..... 43.
43. Spores not more than 9 μ long; pileus white-hoary, lutescent to rusty orange. *C. multiformis.*
43. Spores more than 9 μ long ..... 44.
44. Pileus lilac, becoming brownish, gills pallid or with a slight pinkish tinge. *C. arenicola.*
44. Pileus and stipe white ..... *C. albidus.*
44. Pileus yellowish, brownish or red at first ..... 45.
45. Pileus light red, pellicle not bitter ..... *C. sublateritius.*
45. Pileus yellowish, pellicle bitter ..... *C. aleruiosmus.*[2]

NEW OR REDESCRIBED BULBOPODIA

Cortinarius amnicola Smith, sp. nov. Pileus 4.5–7 cm. latus, convexus demum planus, viscidus, laete luteus et aurantio-virgatus; lamellae lilacinae, confertae, angustae; stipes 4–7 cm. longus, 8–12 mm. crassus, marginato-bulbosus, solidus, deorsum laete luteus, sursum lilacinus; sporae 10–12 × 6–7 μ.

Pileus 4.5–7 cm. broad, broadly convex to subhemispheric when young, becoming plane, viscid, appearing as if streaked with agglutinated fibrils, color evenly "capucine yellow" or with "Mikado orange" streaks (very brilliant yellow, often streaked with orange-yellow), veil remnants sparse and merely scattered along the margin; flesh pallid in the pileus, "pale vinaceous lilac" in the upper part of the stipe, odor faintly fragrant, taste mild in all parts; lamellae "pale vinaceous lilac" (pale lilac) at first, slowly changing to "vinaceous fawn" (pale lilac-brown), sometimes "vinaceous lavender" (dull lilac) in partly expanded pilei, moderately close, deeply adnexed, narrow (5 mm. ±), moderately close, edges even; stipe 4–7 cm. long, 8–12 mm. thick, solid but becoming spongy in the bulb in age, bulb up to 2 cm. broad and depressed-marginate, surface "pale vinaceous lilac" toward the apex, bright yellow both inside and out toward the base, silky from the veil remnants, fragments of universal veil adhering to the margin of the bulb and nearly "Mikado orange" in color, base of bulb and mycelium "citron-yellow," cortina scanty and very pale yellowish; spores 10–12 × 6–7 μ, tuberculate-roughened, pale russet in KOH, narrowly amygdaloid; basidia four-spored; cheilocystidia and pleurocystidia not differentiated; pileus-trama with a thick gelatinous pellicle made up of narrow (2–4 μ) contorted hyphae with dull lilac contents when mounted in KOH, contents rusty brown in chloral hydrate and iodine.

Scattered on humus under butternut, walnut, and basswood on low ground along streams, Ann Arbor, Sept. 11 (*A. H. Smith 15308*), and Sept. 15, 1940 (*A. H. Smith 15381*—TYPE).

The pilei of this species assume a dark vinaceous red color ("ocher-red") when dried in contrast to the bright or pale yellow of dried pilei of *C. calochrous*. The brilliant colors of the stipe, if preserved by careful drying, fade in short time, and in herbarium specimens soon become a dull grayish-olivaceous hue. *C. amnicola* is distinct from *C. calochrous* as the latter is known

[2] *Cortinarius aleuriosmus* sensu Kauffman is here keyed out as *C. Boudieri;* the true *C. aleuriosmus* is not yet known from North America.

in the United States, by the color change which takes place as specimens are dried, by its larger spores and persistent lilac color in the apex of the stipe. My concept of *C. calochrous* is based on Kauffman's (3) account and on material which corresponds to it which I have collected both in Michigan and along the west coast. Lange's (5) concept and that of Kauffman agree closely and certainly apply to the same species. Henry (1) on the other hand has described a species practically identical with *C. amnicola* under the name *C. calochrous*. I have no information on the colors assumed in drying by the pilei of his specimens, so no comparison can be made on that point. Since Fries and most European workers after him have not placed a fungus with persistent lilac colors in the apex of the stipe in *C. calochrous*, I have described my collections as a different species. A sharp difference in spore-size has been observed between the local collections of *C. amnicola* and *C. calochrous*. This difference is not so apparent when one examines the descriptions of the latter, however. The spores of *C. calochrous* are generally given as 10–11 μ long by European authors. Kauffman (3) stated that they seldom measured 10 μ long. In my western specimens they measure 8–10.5 μ, are very pale brown in KOH and only slightly roughened. However, when compared under the microscope, the spores of *C. amnicola* are larger, darker, more tuberculate and more amygdaloid in shape. These differences appear to me to be taxonomically significant.

Cortinarius arenicola Smith, sp. nov. Pileus 3–5 cm. latus, convexus demum subplanus, viscidus, lilaceus demum sordide lilaceus vel brunneo-maculatus; caro albida; lamellae pallidae demum sordide incarnato-brunneae; stipes 3–5 cm. longus, 8–10 mm. crassus, marginato-bulbosus, lilaceus; sporae 9–11 (12) × 5.5–6.5 μ.

Pileus 3–5 cm. broad, convex, becoming plane or the disc flattened and the sides arched, viscid, "vinaceous lilac" over all at first, fading slowly to "pale vinaceous lilac" or pallid in spots where covered by leaves, margin inrolled and delicately white fibrillose from the pallid cortina, sometimes with small spot-like scales over the disc, old pilei occasionally developing sordid brownish spots; flesh white or faintly lilac just beneath the cuticle, no color change when bruised, odor none, taste mild; lamellae close, moderately broad (5 mm. ±), sharply and deeply adnexed, 2–3 tiers of short individuals, color in button stages "pale vinaceous fawn" (pallid), soon sordid brownish, at maturity near "fawn-color," edges whitish and serrulate to eroded; stipe 3–5 cm. long, 8–10 mm. thick, equal above a small depressed-marginate bulb, solid, flesh lilac near the periphery, whitish in the center, surface evenly "vinaceous lilac" over all, base of bulb paler lilac to whitish, cortina white and causing the surface of the stipe to appear whitish in young stages; spores 9–11 (12) × 5.5–6.5 μ, amygdaloid, dark rusty brown under the microscope in KOH, tuberculate; basidia four-spored; cheilocystidia and pleurocystidia not differentiated; pileus with a gelatinous pellicle, the hyphae 4–5 μ thick and yellowish cinnamon in KOH.

Singly under sassafras, in a dry sandy open woods, Waterloo Project,

Waterloo, Sept. 12, 1940 (*A. H. Smith 15315*—TYPE). Known only from the one locality.

The outstanding characters of *C. arenicola* are the rosy-lilac colors of pileus and stipe, the pallid gills, the very small but depressed-marginate bulb, and spores. *C. olympianus* can be readily distinguished when fresh by the pale bright lilac color of the young gills and clearer color of the pileus. Its pilei dry whitish instead of lilac-brown as in *C. arenicola*. The difference in habitat, of course, is striking but in my estimation is not taxonomically significant.

C. arenicola is distinct from *C. caerulescens* in its pallid gills which become vinaceous brown ("fawn-color") as they mature. The colors of the pileus and stipe also differ from those generally attributed to *C. caerulescens*. *C. olympianus* and *C. caerulescens* have the same appearance when dried but differ sharply in spore size. Specimens of *C. arenicola* dry differently from either of these two and have spores intermediate in size. *C. Dionysae* has the same stature as *C. arenicola* and the same sized spores but differs in the color of the gills and in having a distinctive odor. *C. sodagnitus* has larger spores and lilac gills which are apparently similar in color to those of *C. calochrous*. *C. nemorosus* sensu Henry has larger spores, 13–14 × 6.5–7 μ, and *C. dibaphus* sensu Henry has lilac gills and larger spores.

CORTINARIUS BOUDIERI Henry. Pileus 5–13 cm. broad, broadly convex to nearly plane when young, the margin strongly inrolled, sometimes becoming plane, sometimes with a low obtuse umbo, occasionally the margin becoming wavy but frequently remaining decurved and inrolled, surface viscid to glutinous, the margin often streaked with the fibrillose remains of the veil, the disc often developing spot-like scales, otherwise glabrous, evenly colored, near "pale olive-buff" or pale grayish buff over all when young (colors not matching well in Ridgway), with a tinge of lilac pervading, soon developing vinaceous brown colors either on the disc or along the margin or over all, color then more or less "vinaceous buff" or "avellaneous" but tending toward "fawn-color" (colors very sordid pale vinaceous tawny to avellaneous, no good match in R.), spot-like scales sometimes darker; flesh thick and firm, "pale brownish drab" (sordid brownish lilac), sometimes faintly yellowish near the apex of the stipe, becoming paler but retaining a lilac-brown tinge, odor none, taste mild, no color change when cut or bruised (sordid darker brown or yellowish around the wormholes); lamellae "pale vinaceous drab" to "light vinaceous drab" (dull purplish brown), changing very slowly to sordid pale cinnamon-brown or nearly "army-brown," not staining when bruised, close, 2–3 tiers of short individuals, rather narrow, (8 mm. in a 12 cm. cap), sharply adnexed, edges a bit eroded at times; stipe short, 2–4 (7) cm. long, (10) 15–30 mm. thick above the broad (3–5 cm.), flat, marginate but not depressed bulb, solid, flesh very firm and sordid watery lilac (very pale), soon lilac-buff or whitish (similar to that of the pileus), surface very silky and pale lilac, cortina whitish and not copious, bulb whitish and flattened on the underside, universal veil scanty, when well developed adher-

ing along the margin of the bulb in inconspicuous patches, the margin of the bulb sometimes sordid yellowish as if stained; spores 9–11 × 5–6 μ, very rarely 12 × 7 μ; subamygdaloid, dark rusty brown under the microscope, rather coarsely tuberculate; basidia four-spored, hyaline or slightly yellowish in KOH; cheilocystidia and pleurocystidia not differentiated; pileus-trama with a gelatinous pellicle of hyaline (in KOH) contorted hyphae 4–6 μ thick.

Cespitose to gregarious in arcs under oak, hickory, basswood and sassafras, Ann Arbor, Sept. 13–17, 1940 (*A. H. Smith 15328, 15330, 15393, 15332, 15382*).

This species has the same stature as *C. purpureophyllus* and also approaches the latter in color. The colors are consistently much paler and duller, however, and there is a slight difference in spore-size as well. Dried specimens of the two species can be very easily distinguished in the herbarium by the reaction of the hymenium to KOH. In *C. purpureophyllus* the basidia become bright pink, near "Rose Doree" whereas in *C. Boudieri* they remain hyaline or pale yellowish. Both species were found in the one locality and compared when fresh as well as after being dried. The reaction of the hymenium in KOH has, of course, been verified by a study of the type of *C. purpureophyllus*.

The white flesh, farinaceous odor and bitter taste of the pellicle of the pileus distinguish *C. aleuriosmus* Maire. In addition, the colors of the pileus in *C. Boudieri* become much darker than those of *C. aleuriosmus* as described by Maire. Maire has given the name *C. Rickenianus* to the species Ricken placed under *C. aleuriosmus*. It appears to me, on the basis of the descriptions, that Ricken's concept of *C. aleuriosmus* and Boudier's of *C. multiformis* represent the same species for which the earliest name is *C. Boudieri*.

Cortinarius calyptrodermus Smith, sp. nov. Figure 1. Pileus 5–10 cm. latus, convexus demum planus, viscidus, fragmentis volvae obtectus, laete caeruleus, demum pallide caeruleus; caro pallide lilacina vel subcaerulea; lamellae intense caeruleae; stipes 5–9 cm. longus, 1–2.5 cm. crassus, marginato-bulbosus, pallide caeruleus demum albido-caeruleus; sporae 10–12 × 6–7 μ.

Pileus 5–10 cm. broad, convex to obtuse in button stages, broadly convex to plane in age, the margin streaked with agglutinated fibrils, whitish to pale lilac in button stages (the universal veil almost completely covering the young cap), the universal veil tissue becoming areolate-cracked and finally aggregated into matted fibrillose patches at least around and over the disc, the disc sometimes covered with a large felt-like calyptra, viscid beneath the remains of the veil or when the latter have been worn away, color "pale bluish lavender" over all in button stages (owing to the colored u. veil), pileus "Vanderpool's violet" (deep violet) beneath the veil, becoming "light full bluish violet" over all at maturity, in age slowly becoming whitish or sordid brownish; flesh pale lilac (like the u. veil) or brighter in the apex of the stipe and there colored like the surface of the pileus, finally becoming very pale lilac or whitish in both pileus and stipe, unchanging when bruised,

moderately thick and firm, odor and taste not distinctive; lamellae moderately close and broadly adnexed, "Vanderpool's violet" when young, retaining this color very persistently and in age only tinged with brown, the edges decidedly eroded; stipe 5–9 cm. long, 1–2.5 cm. thick above the broad marginate bulb, bulb 3–4 cm. broad, pale violet at first from the universal veil remnants, whitish in age, rounded below, violaceous within and later becoming white, concolorous with the gills above the bulb and beautifully decorated with the remnants of the violet cortina, solid, firm; spores 10–12 × 6–7 μ, subamygdaloid, dark tawny under the microscope in KOH, coarsely tuberculate; basidia four-spored; cheilocystidia and pleurocystidia not differentiated or the former merely slightly larger than the basidia but of the same shape; pileus-trama homogeneous beneath a thin gelatinous pellicle, composed of hyphae 4–7 μ broad which have hyaline to pale vinaceous contents in KOH, at times with a rather strong vinaceous tint throughout the entire thickness of the pellicle.

Gregarious in arcs in a low woods of second growth oak and basswood and various shrubs, Sharron Hollow, Sept. 14, 1940 (*A. H. Smith 15356*—TYPE). Known only from the one locality, but a wagon load of material could have been collected that day. It was the most abundant mushroom in the woods.

One outstanding feature of this species is the mass of white mycelium which surrounds the base of the bulb. This mycelium penetrates through the humus and debris causing much of the latter to be held together in a manner similar to that of *Tricholoma acerbum*. The very well-developed universal veil is, of course, the most conspicuous feature of the fungus. Hundreds of arcs, each containing anywhere from ten to fifty fruiting bodies were observed on Sept. 14, and the veil was a very constant feature. The only other species in which I have observed such a character is *C. calyptratus* from California. The latter is distinguished both by its brownish flesh and smaller spores. *C. praestans* is also said to have a well developed veil which leaves patches of tissue over the pileus, but it does not belong in the subgenus Bulbopodium. I regard the extreme development of such a tissue in viscid Cortinarii as a secondary character lacking any particular phylogenetic significance but furnishing a valuable aid in recognizing the species.

Henry (1) gives the spores of *C. caerulescens* as 10–13 × 6–7 μ, and describes the bulb and surface of the pileus as becoming yellowish in age. I did not observe such color changes in my collection or in any of the material seen in the field at the time. It is very likely that this color change is a good character by which the two can be separated, but I have hesitated to emphasize it. The fruiting bodies of the various species collected along with *C. calyptrodermus* had developed during about ten days of clear weather following a period of very heavy rainfall. In all, the bright colors characteristic of the young stages were unusually persistent in the maturing pilei. Since the change to yellow in *C. caerulescens* apparently develops as the specimens mature and age, this change may have been inhibited by the conditions pre-

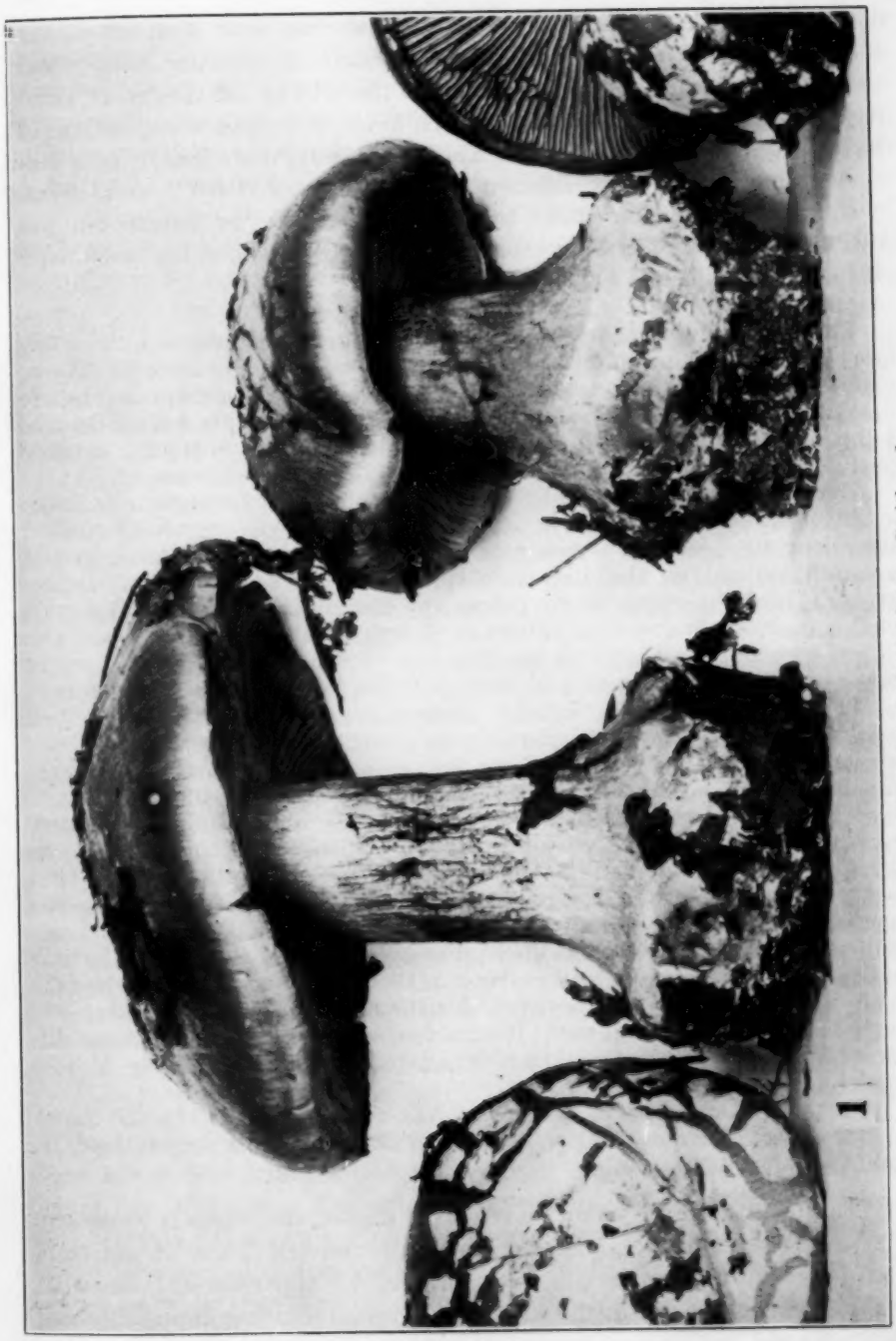

FIG. 1. *Cortinarius calyptrodermus* Smith. ×1.

vailing last September, and *C. calyptrodermus* may show it on subsequent collections. *C. Atkinsonianus* was very abundant in the same locality and showed scarcely any change to reddish on the pilei of old specimens. Ordinarily this change is very conspicuous. However, in drying, the specimens of the latter species did turn reddish. Those of *C. calyptrodermus* dried a dull blue and now appear very different from dried material of *C. caerulescens.*

C. michiganensis is similar to *C. calyptrodermus* in stature but has smaller spores and generally a shorter stipe. *C. caesiocyaneus* has much paler gills when young and a glabrous pileus in age.

Cortinarius citrinipedes Smith, sp. nov. Figure 3. Pileus 4–7 cm. latus, late convexus, demun planus, viscidus, sordide olivaceo- vel luteo-fibrillosus, glabrescens, obscure purpureo-brunneus demum subargillaceus; caro obscure lilacina; lamellae obscure lilacinae demum argillaceae; stipes 4–6 cm. longus, 1–2 cm. crassus, marginato-bulbosus, solidus, obscure lilacinus, argente fibrillosus; sporae 8–10 (11) × 4.5–5 μ; myceliun olivaceo-luteum.

Pileus 4–7 cm. broad, broadly convex with an inrolled margin, remaining broadly convex or expanding to nearly plane, the margin remaining inrolled for a long time, surface viscid, soon dry, buttons "Isabella color" (sordid greenish yellow) on the disc from the universal veil remnants, "benzo-brown" (dark purplish brown) near the margin, sometimes with a pale pruina over all causing it to appear as though with a lilac-olivaceous sheen, in age becoming clay color on the disc or with a persistent greenish yellow cast, sometimes unicolorous and dark purplish brown (when the veil remnants have disappeared), inrolled margin more or less lilac-gray; flesh moderately thick, "dark lavender" (a dull fairly deep lavender) and slowly becoming whitish, not staining where bruised, odor and taste not distinctive; lamellae "dark lavender" when young and slowly changing to "tawny-olive" (dull yellowish brown, never truly yellow), bluntly adnate and very narrow (4 mm. broad ±), crowded, edges even; stipe 4–6 cm. long, 1–2 cm. thick, with a marginate bulb 3–4 cm. broad, solid, flesh "dark lavender" but becoming whitish, surface pale silvery lilac from the copious lilac-white cortina, universal veil and mycelium around the base of the bulb "greenish yellow" (almost more greenish than yellow) and causing the base of the bulb to be bright greenish yellow in contrast to the other parts; spores 8–10 (11) × 4.5–5 μ, about ochraceous tawny under the microscope in KOH, narrowly amygdaloid, slightly roughened; basidia four-spored; cheilocystidia not differentiated; pileus-trama with a thin gelatinous pellicle made up of contorted hyphae 3–5 μ thick.

Gregarious on humus in oak woods, Ann Arbor, Sept. 11, (*A. H. Smith 15305*—TYPE); Sharron Hollow, Sept. 14 (*15358*), and Ann Arbor, Sept. 16, 1940 (*15395*).

The sordid greenish yellow color on the disc of the pileus is caused by adhering remains of the greenish yellow universal veil. These do not form a tissue as in *C. calyptrodermus,* but rather become appressed and somewhat dispersed giving the disc of the pileus an appressed-fibrillose appearance and obscuring the true color. Beneath the veil-remnants the pileus is evenly

colored. When dried the pilei vary from olivaceous gray to lilac gray on the margin and dark rusty brown over the disc. In none were the colors as bright or as yellowish as in *C. glaucopus*. The dark, dull lavender flesh and also the lavender gills are very characteristic. The bright greenish yellow universal veil and mycelium is in decided contrast to the color of all other parts. These characters in addition to the small spores distinguish the species.

C. velicopia Kauff. is very close to *C. citrinipedes* but is characterized by cheilocystidia, paler bluish colors instead of lavender, and a tendency for the pileus to become yellowish. There is also a slight but appreciable difference in spore size when spores of both are compared under the microscope, and a distinct difference in the color of their universal veils.

Cortinarius squalidus Smith, sp. nov. Figure 4. Pileus 3–6 (8) cm. latus, convexus, demum planus, viscidus, subcanus demum glaber, pallide cinnamomeus demum obscure brunneus; lamellae pallide brunneae nunquam albidae, demum obscure brunneae; stipes 3–5 cm. longus, 10–15 mm. crassus, solidus, bulbosus, sericeo-fibrillosus et pallidus; sporae 7–9 × 4–5 μ.

Pileus 3–6 (8) cm. broad, convex, obtuse in age, the margin incurved or bent in slightly and usually remaining decurved, at first furnished with inconspicuous patches of white fibrils from the universal veil (especially near the margin), at times faintly canescent over all, usually variously streaked or with irregular watery spots, viscid, color "cinnamon" over all but becoming a dark, dull brown (nearly "cinnamon-brown"); flesh moderately thick and brittle, "pale pinkish buff," watery and darker (near "cinnamon-buff") in the stipe, odor and taste mild; lamellae very pale dull brown when very young (definitely not white), almost concolorous with the pileus in age, adnexed, close but distinct, moderately broad (5–6 mm. ±), edges nearly even; stipe 3–5 cm. long, 10–15 mm. thick, equal above the flanged basal oblique bulb, solid, pallid within, exterior whitish and silky overall, cortina white and scanty, universal veil scanty, bulb 2 cm. ± broad and pointed below; spores ellipsoid, slightly roughened or practically smooth, sordid ochraceous tawny under the microscope in KOH, 7–9 × 4–5 μ; basidia four-spored; cheilocystidia and pleurocystidia not differentiated; pileus-trama with a distinct but thin gelatinous pellicle, the hyphae 3–5 μ thick and hyaline, the floccose tissue immediately beneath the pellicle made up of hyphae with pale cinnamon-brown contents, the remainder of the flesh hyaline.

In arcs or clumps in an oak-hickory woods, Ann Arbor, Sept. 15 (*A. H. Smith 15379*—TYPE); Sept. 16 (*15411, 15399*); and Sept. 28, 1940 (*15546*).

Cortinarius squalidus is very similar in its characters to *C. allutus* Sec. sensu Lange, but from the available information cannot be referred to it. Henry has divided that species into two varieties, var. *lutea* and var. *rufescens*. *C. squalidus* is never bright yellow in any part so it cannot be referred to the former, and it does not become reddish in age or when dried so it cannot be referred to var. *rufescens*. *C. squalidus*, as its name indicates, is a very dull brown fungus presenting a rather sordid appearance in all except

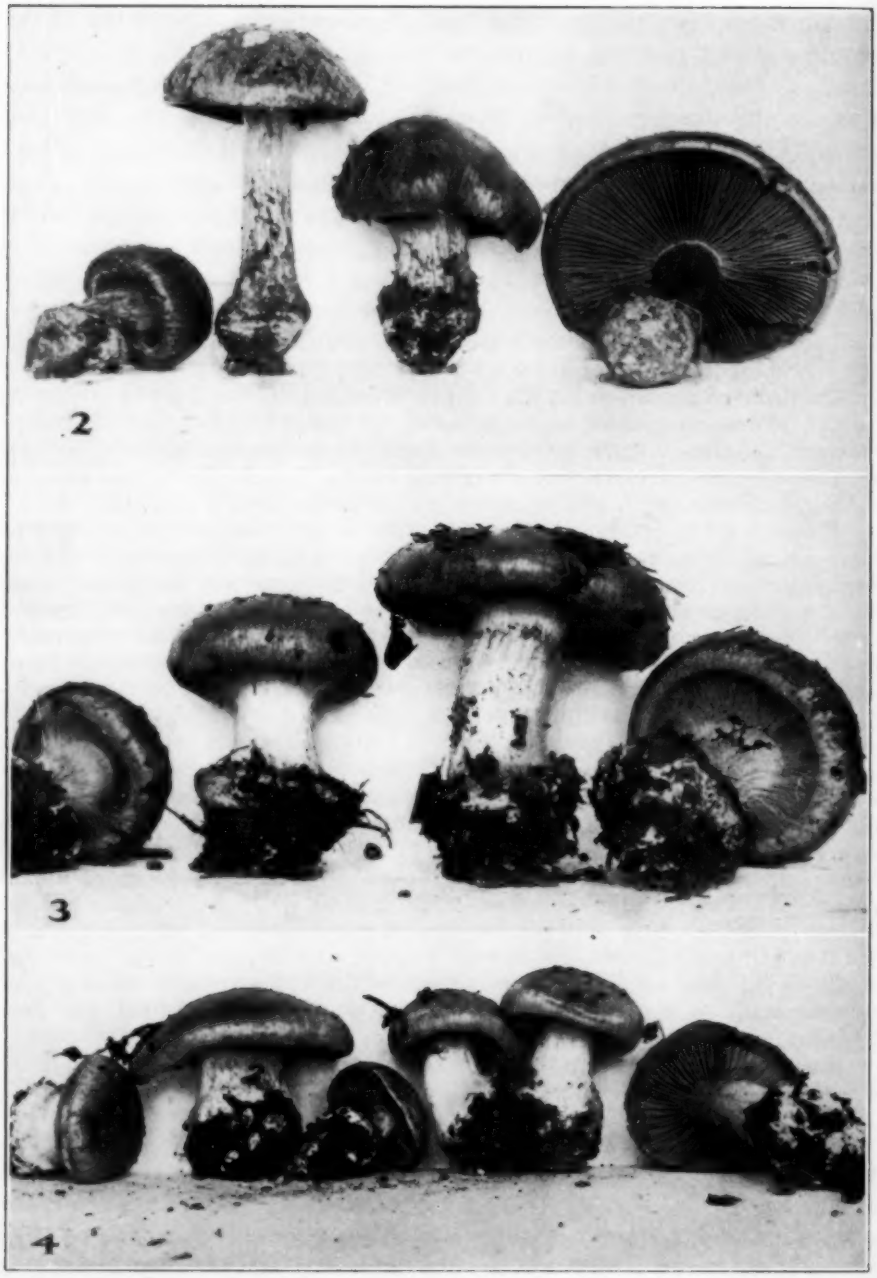

FIG. 2. *Cortinarius subsolitarius* Smith. × 0.7. FIG. 3. *Cortinarius citrinipedes* Smith × 0.7. FIG. 4. *Cortinarius squalidus* Smith. × 0.7.

the button stages. *C. nappus* as described by Henry (1) is apparently close but has spores 9–12 × 5.5–6 μ and is generally a more robust species. In addition, its colors tend to be yellow or yellowish in places.

Cortinarius subsolitarius Smith, sp. nov. Figure 2. Pileus 4–6 (10) cm. latus, obtusus, demum subumbonatus vel planus, glaber, virgatus, obscure violaceus, demum subolivaceo-violaceus; lamellae obscure violaceae demum brunneo-tinctae, angustae, adnatae; stipes 3–5 cm. longus, 10–15 mm. crassus, obsolete bulbosus, obscure violaceus; sporae 7–9 × 4 μ.

Pileus 4–6 (10) cm. broad, obtuse, becoming obtusely umbonate to nearly plane, the margin remaining incurved for a long time, surface viscid, glabrous but conspicuously streaked or blotched or with irregular watery spots, occasionally with fibrils along the margin, color "dull bluish violet (2)" the watery streaks darker (very dark violet), sometimes "dark dull bluish violet (2)," developing a distinct greenish gray tinge in age and fading only slightly, sometimes yellowish on the disc in extreme age; flesh thin, "pale campanula-blue" but becoming more greenish blue in age, "dark dull bluish violet" and watery punctate in the stipe, concolorous with the pileus in age, taste mild, odor faint and earthy, no color changes noted on bruised portions; lamellae "dark dull bluish violet (2)" and remaining so a long time, in unopened buttons "dusky blue-violet," in age merely tinged cinnamon-brown from the spores, close, adnate but tending to become adnexed, narrow to moderately broad, edges crenulate; stipe 3–5 cm. long, 10–12 mm. thick at the apex, up to 20 mm. at the base, solid, bulb marginate at very first but stipe soon merely clavate and hardly flanged at the base, concolorous with the gills and silky, cortina at first "dark dull bluish violet" fading only slightly; spores 7–9 × 4 μ, subamygdaloid, rusty brown under the microscope in KOH; basidia four-spored; cheilocystidia scattered, cylindric, hyaline, 28–39 × 4–6 μ; pleurocystidia not differentiated; gill-trama pale sordid vinaceous in KOH, especially near the gill-edges; pileus-trama homogeneous beneath a gelatinous pellicle, the hyphae of the pellicle pale yellowish in KOH, a region of yellowish brown floccose tissue immediately beneath the pellicle.

Scattered to gregarious on humus in oak-hickory woods, Ann Arbor, Sept. 11 (*A. H. Smith 15307*), Sept. 16 (*A. H. Smith 15377*—TYPE), and Sept. 16, 1940 (*15400*).

I have collected occasional specimens of this species in the vicinity of Ann Arbor for the past ten years and referred them doubtfully to *C. aggregatus* Kauff. because of the small spores. During September, 1940, both *C. subsolitarius* and *C. aggregatus* were found, the latter very abundantly, and a comparison of fresh specimens was made. The outstanding single feature of *C. subsolitarius* is the very deep, heavy violaceous persistent color of all its parts. As the fruiting bodies age, a greenish cast develops but the color in general does not become appreciably lighter. In a few old pilei yellowish spots developed on the disc and the flesh was yellowish around the wormholes. The bulb is very small and soon obsolete, being about as inconspicuous as that of *C. corrugatus*. *C. aggregatus* fades to a much paler color, has a

larger bulb and occurs in great quantities. In all of the specimens of *C. aggregatus* which I have seen, the colors of young individuals were paler than those of *C. subsolitarius*. *C. glaucopus* and its forms have the small spores but lack the uniform dark violet shades and show a very decided change of color from youth to old age. All the *C. glaucopus* which I have collected dried a greenish to rusty yellow over the pileus. Specimens of *C. subsolitarius* dry either dull violet or dull violaceous brown.

NEW OR REDESCRIBED SPECIES OF PHLEGMACIUM

CORTINARIUS CLARICOLOR Fr. sensu Ricken.? Pileus 5–9 cm. broad, convex to obtusely umbonate, nearly plane in age, the margin often remaining slightly decurved, sometimes repand and wavy or scalloped, surface glabrous and viscid, at times decorated with scattered fibrils along the margin, color "ochraceous tawny" (yellowish brown) over the disc and "warm-buff" (very pale buff-yellow) along the margin, sometimes with a canescent appearance as in *Pholiota caperata;* flesh thick and firm, whitish to faintly yellowish, unchanging, taste mild, odor fragrant when young pilei are cut; lamellae at the very first with a caesious tinge, soon pallid or "avellaenous" and finally pale "clay-color," close, 2–3 tiers of short individuals, broad (8–12 mm.), bluntly adnate at first, becoming adnexed in age; stipe stout, 8–10 (12) cm. long, 10–18 mm. thick at the apex, clavate-bulbous, the bulb 2.5–4 cm. thick, solid, texture cottony in the interior, whitish or faintly yellowish within, surface evenly colored like the context and densely silky from the copious cortina, with pale yellowish subannulate bands over the lower portion in age from the broken universal veil, u. veil white at first but remnants slowly lutescent, in age the flesh becoming slightly rusty brown around the wormholes or the surface brownish where handled; spores 9–11 (12) × 5–6 (7) μ, dark rusty brown under the microscope in KOH, coarsely tuberculate; basidia four-spored; cheilocystidia and pleurocystidia not differentiated; pileus-trama with a thick gelatinous pellicle, the hypae 4–5 μ thick and yellowish in KOH.

Gregarious on humus in low or upland oak woods, Sharron Hollow, and Ann Arbor, Sept. 14 and 16, 1940 (*15361, 15418*).

From his comments (2) it is quite clear that Kauffman's collections from New York, on which he based his report, represent some other species, which one I am not prepared to say. The small spores, subemarginate bulb and lack of a universal veil do not allow his collections to be placed here. In my specimens the white-fibrillose remains of the universal veil showed a tendency to become yellowish in age. This is not in accordance with the European concepts. The bands on the lower part of the stipe were never as highly colored as in *C. luteoarmillatus*, however. The gills of the younger specimens in all of my collections, as well as on all of the material I observed growing in the woods, consistently showed a caesious tinge. Many European authors described the young gills as pallid and slowly becoming brownish. Konrad and

Maublanc (4, pl. 126) give the spores as 11–15 × 6–8 μ, a rather serious discrepancy in this genus and indicating that their species is not that of Ricken.

Because of the zones on the stipes of old specimens some might be tempted to refer my material to *C. triumphans*. In my collections of the latter, however, the universal veil was distinctly colored in button stages and the pileus was also brighter.

Cortinarius luteoarmillatus Smith, sp. nov. Pileus 3–5 cm. latus, obtusus, demum convexus, viscidus, glaber, ad marginem fibrillosus, pallidus vel albido-argillaceus; lamellae sordide albidae demum argillaceae; stipes 5–6 cm. longus, 8–15 mm. crassus, clavatus, deorsum luteo-armillatus, sursum albidus et albido-fibrillosus; spores 8–10 × 5–6 μ.

Pileus 3–5 cm. broad (all rather young), obtuse, the margin incurved, becoming broadly convex as they mature, surface viscid, glabrous, with scanty remnants of a cortina along the margin, spot-like scales developing on the disc, color "cinnamon-buff" when young, "pinkish buff" in age (pale brownish buff) the disc usually shaded a bit darker than the margin; flesh thick, firm, hard, odor faintly fragrant, taste subnauseous, no color changes when cut or bruised; lamellae moderately close, adnexed, narrow (all young) 2–3 tiers of short individuals white to "tilleul-buff" (whitish), slowly becoming sordid brownish, edges even; stipe 5–6 cm. long, 8–15 mm. thick at the apex, clavate bulbous, (2 cm. thick at the base), rounded below and furnished with white rhizomorphs, the lower enlarged area with delicate yellowish zones of fibrils from the remains of a universal veil, cortina white and copious, apex loosely silky-fibrillose and appearing white because of the veil-remnants, solid and whitish or pale buff within; spores 8–10 × 5–6 μ, ellipsoid, nearly smooth, very pale yellowish brown under the microscope in KOH; basidia four-spored; cheilocystidia and pleurocystidia not differentiated; pileus-trama with a gelatinous pellicle made up of hyphae 3–4 μ thick and nearly hyaline when mounted in KOH.

Gregarious on muck soil in low woods, Sharron Hollow, Sept. 14, 1940 (*A. H. Smith 15360*—TYPE).

This species appears to be well characterized by the yellow zones of fibrils distributed over the lower third of the stipe, the whitish gills and very pale buff pileus along with the small spores. Were it not for the yellow zones left on the stipe by the universal veil, I should be inclined to identify my collection with *C. lustratus* Fr. or *C. sebaceus*. The spores and gelatinous pellicle of the pileus exclude *C. albidifolius* Pk., a species with apparently the same stature as *C. luteoarmillatus*.

C. triumphans has similar but darker yellow bands on the stipe, but is readily distinguished by the colors of both pileus and gills. There appear to be several forms very similar to *C. triumphans* in North America. During the past season I collected one with spores 7–9 μ long and 6–8 μ wide which may be a distinct species. Its gills were pale caesious at first as in typical *C. triumphans*. My material, however, was not sufficient for a critical study.

FIG. 5. *Cortinarius claricolor* Smith. ×0.7. FIG. 6. *Cortinarius fumosifolius* Smith ×0.7.

NEW AND REDESCRIBED SPECIES OF INOLOMA AND TELAMONIA

CORTINARIUS OBLIQUUS Pk. Pileus 7–10 cm. broad, very broadly convex, the margin decurved, becoming plane with an arched margin or the margin slightly uplifted thus creating a broad shallow central depression, surface dry and appressed silky fibrillose, the margin fringed or with adhering fibrillose patches, color "pale vinaceous fawn" (pallid with just a tinge of flesh-color) in age becoming darker and near "vinaceous buff" (darker pinkish brown); flesh thick and firm, "pallid purple-drab" in the stipe and along the gills, taste mild, odor fragrant; lamellae narrow (7–8 mm. in caps 10 cm.

broad), close to crowded, 2–3 tiers, depressed adnate to adnexed, with a decurrent tooth in age, "dark vinaceous brown" (dull purplish red) in youngest specimen (no buttons available), becoming dark cinnamon brown at maturity, edges eroded; stipe 7–12 cm. long, 1–2.5 cm. thick above the almost marginate bulb (2–3.5 cm. broad), solid, pallid purplish within, surface densely silky fibrillose from the remains of the cortina, toward the apex "light heliotrope-gray," (pale purplish gray—with only a tinge of vinaceous), pallid downwards, with a short sheath of matted fibrils formed by the universal veil remnants and terminating at the margin of the bulb; spores 8–10 (11) × 5–6.5 μ, ellipsoid, tuberculate, dark rusty brown in KOH; basidia four-spored, more or less sordid vinaceous brown when revived in KOH; cheilocystidia and pleurocystidia not differentiated; gill-trama and pileus-trama homogeneous.

Gregarious under beech, La Badie Lake, near New Hudson, Oakland Co. Sept. 23, 1940 (*15438*). The above description was taken from this collection.

The form described here differs so much in general proportions from typical specimens of the species that it seemed best to give a complete account of it. Large fruiting bodies such as this are known to occur in other species of Cortinarius and also in other genera of agarics. This is the second time I have encountered this particular form of *C. obliquus* in Oakland County, Mich. It was found first near Milford on Aug. 23, 1937. Both collections were made during dry weather following a period of very heavy rainfall.

Cortinarius subtestaceus Smith, sp. nov. Figure 7. Pileus 3–7 cm. latus, obtusus vel convexus, demum subplanus, saepe subdepressus, siccus, innate fibrillosus, pallide testaceus demum obscure testaceo-brunneus; caro aquose brunnea, demum pallida; lamellae argillaceae demum ochraceo-brunneae, subconfertae, latae, adnatae; stipes 6–14 cm. longus, 10–15 mm. crassus, clavatus, deorsum testaceo-cinctus, sursum sericeus et pallidus, solidus; sporae 9–11 (12) × 6–7 μ.

Pileus 3–7 cm. broad, obtuse to convex, expanding to plane or broadly convex, sometimes with a low umbo, surface dry and densely innately fibrillose under a lens (appearing glabrous to the naked eye), in age the fibrils arranged in small patches (as seen under a lens) but not becoming scaly, occasionally rimose over the disc in extreme age, margin delicately fringed with fibrils at first, color evenly "fawn-color" when young (rather bright vinaceous brown), becoming darker and near "walnut-brown" in age (full vinaceous brown); flesh watery brownish (pinkish buff) soon pale pinkish buff or pallied (a bit more vinaceous brown in the stipe), firm, fairly thick, taste mild, odor faintly acidulous; lamellae "clay-color" to near "buckthorn-brown" in unopened buttons (sordid yellowish brown), becoming "ochraceous tawny" at maturity, (tawny-brown), close but becoming nearly subdistant, 68–76 reach the stipe, 1–2 tiers of short individuals, moderately broad (6–7 mm.), broadest near the stipe, adnate, becoming shallowly adnexed; edges even; stipe 6–14 cm. long, 10–15 mm. thick at the apex, enlarged below to a narrowly clavate bulb and tapered to a point at the base, sometimes nearly fusiform or in age nearly equal and somewhat rooting, lower one third to one half covered by bands of "army-brown" to "fawn-

color'' universal veil remnants, cortina white and silky and the upper half of the stipe whitish to pallid because of a coating of appressed, silky fibrils; spores 9–11 (12) × 6–7 μ tuberculate, ellipsoid, pale yellowish brown under the microscope in KOH; basidia four-spored; cheilocystidia none; gill-trama brownish-cinnamon when revived in KOH; flesh of pileus homogeneous and paler than the gill-trama.

Gregarious on humus in low woods, La Badie Lake, Oakland Co., Sept. 24 (*A. H. Smith 15458*—TYPE), and Ann Arbor, Sept. 28, 1940 (*15548*).

FIG. 7. *Cortinarius subtestaceus* Smith. × 0.7.

The surface of the pileus in this species has a dry appearance, but the flesh is watery punctate and changes color appreciably when it fades. Consequently the fungus is placed in Telamonia along with *C. armillatus*. Although the descriptions of these two read somewhat alike, one would never confuse the species in the field. *C. armillatus* is very common in northern Michigan, where I have collected it on numerous occasions. Its veil remnants are a much brighter red, its stature is much more robust, the stipe much thicker at the base, and its spores are much darker brown when mounts of both in KOH are compared under the microscope. The most conspicuous difference, however, is in the color of the universal veil. At first I was inclined to consider the collections cited above as belonging to *C. haematochelis*. Bresadola has given the length of the spores of that species at 7–8 μ long, and, judging by his illustration, its universal veil is colored more like that of *C. armillatus*. Some consider *C. haematochellis* as a synonym of *C. armillatus*.

C. paragaudis also has a somewhat similarly colored though poorly developed universal veil, but its spores are smaller, its stipe is equal and becomes dark purple at the base. Both *C. paraguadis* and *C. armillatus,* according to my experience, grow in conifer or mixed conifer and hardwood forests. *C. subtestaceus* was found on low ground under ash, elm, bur-oak and soft maple. The only conifers within a radius of one hundred yards were larch trees well out in the bog. *C. veregregius* Henry apparently has the same type of veil as *C. subtestaceus,* but its gills are described as brighter yellow and its spores are smaller and not ellipsoid.

Cortinarius fumosifolius Smith, sp. nov. Figure 6. Pileus 2–3.5 cm. latus, convexus demum subplanus, albo-fibrillosus, subglabrescens, obscure purpureo-brunneus, hygrophanus demum pallide argillaceus; lamellae fumosae, demum argillaceae vel sordide alutaceae; stipes 2–3 cm. longus, 4–6 mm. crassus, bulbosus, fibrilloso-volvatus, cavus, dense albido-fibrillosus; sporae 7–9 × 4–5 μ.

Pileus 2–3.5 cm. broad, broadly convex or with a flattened disc at first, in age broadly convex or with a low obscure umbo, surface appearing dry and whitish because of a dense covering of loose white fibrils, in age the fibrils becoming aggregated into patches scattered over the entire surface, margin ± fringed at first, color evenly "benzo-brown" (dull purplish brown) beneath the fibrils, the surface moist, hygrophanous and fading to sordid "pinkish buff," usually remaining more or less covered by the white fibrillose patches in age; flesh thickish, fragile, watery, "benzo-brown" but soon fading to pale sordid buff, odor and taste not distinctive; lamellae "light drab" (brownish gray) when young, sordid "clay-color" in age (pale alutaceous), adnate, becoming slightly adnexed, often with a decurrent tooth, close, 40–44 reach the stipe, 1–2 tiers of short individuals, moderately broad (3–4 mm.); stipe short, 2–3 cm. long, 4–6 mm. thick at the apex, base with more or less of a rounded bulb, fragile, hollow, watery, universal veil very copious and adhering to the bulb forming a volva-like fringe around it, appressed-silky above the bulb and with a whitish sheen, tinged violaceous brown beneath the fibrils (nearly concolorous with but paler than the pileus), cortina moderately copious; spores 7–9 × 4–5.5 μ, ellipsoid, dark rusty brown in KOH under the microscope, tuberculate; basidia four-spored; cheilocystidia and pleurocystidia not differentiated; gill-trama homogeneous, cells pallid in KOH; pileus-trama with a differentiated surface-layer of inflated cells 15–30 μ thick (tangential sections) which give a pseudoparenchymatous appearance similar to that in most species of Psathyrella, beneath it the tissue compact and floccose and made up of narrower hyphae, universal veil remnants resting on this layer and made up of narrow filamentous hyphae.

Gregarious under rhododendrons, Arboretum, Ann Arbor, Sept. 7, 1940 (*Mr. and Mrs. Paul Marshall Rea and A. H. Smith 15266*—TYPE). Known only from the type locality.

This *Telamonia* has so many unusual characters that it is hard to believe that it has not been previously described. The gray gills, the practically

marginate bulb (and development similar to that of species of Bulbopodium), the copious universal veil and the structure of the pileus are outstanding in this subgenus. The surface of the pileus is covered by universal veil remnants. These consist of hyphae 6–10 μ thick and with cells 50–100 μ long. The cuticle of the pileus is composed of pale brownish hyphae radially arranged and with the cells 15–30 μ thick and 30–60 μ long. This type of organization of the surface-layer in a Cortinarius is unique. I have encountered a rather large series of species in Inoloma which have marginate bulbs and a development comparable to that of the Bulbopodia, but only one other in Telamonia, and that one is still unidentified. More than likely *C. fumosifolius* was introduced. It is one of the few agarics I have collected on the compost around the rhododendron plantings in our local arboretum.

University of Michigan Herbarium
Ann Arbor, Michigan.

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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Beginning with this issue the Index to American Botanical Literature is classified under 8 headings as follows: Plant Taxonomy and Floristics (exclusive of fungi); Morphology (including anatomy, and cytology in part); Plant Physiology; Mycology and Phytopathology; Genetics (including cytogenetics); Ecology and Plant Geography; General Botany (including biography). It is realized that some articles do not fall readily in any of these classifications, and users of the Index interested in a particular topic are requested to examine also classifications which may include closely related topics. The editor and bibliographer will welcome suggestions and criticisms on the usefulness of the new arrangement.

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